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Investigating the effects of management in temperate broadleaved woodland on bats and their insect prey

INVESTIGATING THE EFFECTS OF MANAGEMENT IN TEMPERATE BROADLEAVED WOODLAND ON BATS AND THEIR INSECT PREY

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ABSTRACT

Woodland is an important natural resource providing wood-derived biomass for use as a carbon lean source of heating and electricity. The role of biomass in reducing our dependence on fossil fuels should not be underestimated, nor should the potential negative impacts on biodiversity as land managers are incentivised to bring under-managed woodland back into production to meet renewable targets. The effect of woodland management on wildlife needs more scientific research. In this thesis, I investigate the influence of the silvicultural practice involving selective thinning of woodland over time on bats and their insect prey, and use emerging technologies to identify the ecological requirements of a woodland specialist bat species at different spatial scales.

When compared to unmanaged woodland (minimal intervention and underutilised), bat species richness was higher in managed woodland (selective thinning) because uncluttered understory vegetation provided opportunities for edge and open foraging bats, in addition to woodland interior specialists. Common and adaptable edge foragers were more active in managed woodland. Interior foragers and tree-roosting bats were more active in unmanaged woodland and often absent from managed woodland. Bats responded positively to standing dead trees and tree cavities, and to a relatively open and heterogeneous canopy architecture. Standing dead trees were three times more abundant, and tree cavities five times more frequent in unmanaged woodland. Canopy architecture was similar between managed and unmanaged woodland. Bats and insects had contrasting non-linear temporal responses to time since last management with bat activity reducing, and insect numbers peaking in early stage successional woodland. The woodland-dwelling bat *Barbastella barbastellus* roosted primarily in ancient semi-natural broadleaved woodland which contained more tree cavities than adjoining younger plantation woodland. High energetic demands of pregnant and lactating bats influenced roost selection and behaviour. *B. barbastellus* specialises in feeding on moths. Linear landscape features such as hedgerows provide food for moth larvae and were used by *B. barbastellus* for feeding on adult moths.

Bats respond well to characteristics that form in old age woodland. The relatively low frequency of standing dead trees and number of cavities in shorter rotation production woodland limits its value to bats. Tree roost availability and canopy architecture characteristics can be encouraged in young woodland by minimal intervention management, or in production woodland through positive thinning management. Improving *B. barbastellus* roosting and foraging habitat will conserve habitat suitable for all developmental stages of their moth prey.

AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Andrew Carr

Signed: ……. Date: …….

DISCLOSURE

Chapter 3 uses some raw field data taken, with permission, from a PhD thesis (Zeale, 2011) combined with field data collected by myself. All desktop measurements were re-calculated and additional airborne LiDAR imagery measurements included before the full dataset was analysed. Justifications for combining this existing raw field data with data collected by myself are (i) that meta-analysis review of papers exploring roost selection by forest-dwelling bats advises at least three years of study are needed to avoid conclusions based on years with unusual amounts of precipitation or warmth or other stochastic events (Naďo and Kaňuch, 2015), and (ii) to allow reproductive status differences between breeding and non-breeding bats to be analysed.

Chapter 4 uses a molecular approach to identify the diet of *B. barbastellus*. DNA extraction and next generation sequencing was undertaken at Queen Mary University of London (QMUL) by Beth Clare. Subsequent bioinformatics was undertaken by myself following training provided at QMUL. The faecal pellets used for prey DNA extraction were collected by myself and were also provided by Ian Davidson-Watts and Jane Harris.

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"the sound of the bat
flying in the thicket
is dark"

Masaoka Shiki (1867 - 1902)

PUBLICATIONS AND CO-AUTHORS' CONTRIBUTIONS

Chapter 3 forms the basis of a published manuscript (Appendix A). AC designed the study with assistance from GJ, AW and MZ. AC and MZ collected radio tracking data on *B. barbastellus* (AC pregnant, lactating and non-breeding bats; MZ post-lactating and non-breeding bats). AC and MZ collected field data on woodland structure. AC collected and processed GIS data. AC processed airborne LiDAR data with assistance from JF. AC performed all analysis. AC drafted the manuscript. JF, MZ, AW and GJ edited drafts of the manuscript. AC, GJ and MZ secured funding.

During my PhD I had the privilege of working with conservationists from other institutions. Collaboration with the Woodland Trust led to a research project not included in this thesis but was a direct result of my PhD research (Appendix B). The project arose from the development of CCTV to collect *B. barbastellus* roost behaviour data during my second field season. This led to a publication in which AC co-developed the study design with SY. AC supported SY with statistical analysis. SY drafted the manuscript. AC and GJ edited drafts of the manuscript. AC and GJ secured funding for AC.

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CHAPTER 1

General Introduction

1.1 Temperate broadleaved woodland

The terms forest and woodland are interchangeable between countries and regions but typically forests are large continuously wooded areas, and woodlands are smaller fragmented areas. My research area is within the United Kingdom (UK) and all broadleaved habitat in the UK can be considered highly fragmented but otherwise typical of large proportions of north western European broadleaved woodland habitat. In addition, with some exceptions, UK woodland tends to be native broadleaf whereas forest tends to be commercial conifer. Throughout this thesis, I use the term woodland and only specify 'forest' when considering particularly large continuously wooded habitat.

Forest and woodland are among the most biologically diverse systems on Earth (Myers et al., 2000) and arguably the most exploited and degraded by anthropogenic activity. In Europe (including Russia), wooded habitat covers approximately 45% of land area (FAO, 2012) (including boreal forest in the north; hemiboreal, nemoral and mixed forest in East Central Europe; and meso-phytic broadleaved and beech woodland in Western Europe (EEA, 2006)). Western temperate broadleaved woodland (also referred to as temperate deciduous woodland) and oceanic woodland is typically composed of oak (*Quercus* spp.), beech (*Fagus* spp.), birch (*Betula* spp.), and maple (*Acer* spp.) (EEA, 2006). The most obvious characteristic which defines temperate broadleaved habitat, is the seasonal appearance and disappearance of canopy vegetation and the adaptations to these changes by dependent flora and fauna.

More than a quarter of European wooded habitat is classified as primary (i.e. old age woodland that has not experienced significant anthropogenic disturbance) although outside of Russia, centuries of land use and forest management has reduced the amount of primary wooded habitat to 0.7% of Europe's forest area (Sabatini et al., 2018). Most of these forests are protected (89%), but only 46% of them strictly, making them vulnerable to encroachment by logging (e.g. the UNESCO World Heritage Site, Białowieża Forest (Michalak, 2016; Nelson, 2018)). Fifty percent of wooded habitat in Europe is designated as 'in production' (i.e. wood is systematically extracted) (FAO, 2012).

Encouragingly in Western, Central and Northern Europe there is a growing interest for managing forest and woodland (including production, semi-natural and plantation) that are diversity-oriented, mimic natural ecosystem function and provide characteristics that form through natural succession (Lähde et al., 1999; Smith, 2018).

In the UK, woodland (including coniferous forest) accounts for 13% of total land cover (FC, 2015). The amount of old-aged woodland (i.e. ancient woodland defined as woodland, usually old growth, that has been wooded since before 1600 AD, and may or may not have been felled at some time in their history (Peterken, 1974)) remaining in the UK is 2% (FC, 2015). An estimated 85% of these old-aged woodlands do not have legal protection (Tickell and Thackray, 2000) making them vulnerable to exploitation and potential habitat change. Recent increases in woodland planting are increasing total woodland cover (FC, 2010). Forty-four percent of UK woodland is sustainably managed (i.e. has been certified as having management that meets legal and advised components of good practice – discussed in section 1.5) leaving 46% classified as abandoned or under-managed (i.e. a classification given when management practices are unknown and assumed absent) (FC, 2015). Our understanding of the value of managed and under-managed woodland to biodiversity is limited meaning it is difficult for conservationists to confidently assess which management type most benefits wildlife.

1.2 Benefits of managing woodland

Woodlands possibly deliver the greatest number of ecosystem services of any habitat including carbon storage, recreation, timber and a contribution to water regulation (Albon et al., 2014). In 2010 the UK forestry sector contributed £1.7 billion in gross value added (GVA) and directly employed approximately 14,000 people (EE, 2015). Broadleaved temperate woodland has long been exploited for timber and charcoal, resulting in what we now term traditional management (e.g.

coppicing), and many plant and animal species associated with woodland have adapted to the characteristics provided by management (Taylor et al., 2013; Peterken and Mountford, 2017).

Legislation commitments for renewable energy (Renewables Obligation Order, 2015) are stimulating techniques and technologies to reduce our reliance on fossil fuel. Woodfuel (e.g. firewood, charcoal, chips, sheets, pellets, and sawdust) is considered a future major source of biomass energy (FAO, 2010). A shift from traditional woodfuel use at the community level to industrial-scale developments has resulted in a global increase in the amount of land being exploited for woodfuel (FAO, 2010). Industrial-scale electricity generation using wood-derived biomass is well established in Nordic countries and has recently expanded in the UK (FAO, 2010; DRAX, 2018). Technological information transfer to other countries is likely to increase as biomass becomes more price-competitive. Given the recognised environmental benefits of climate change mitigation through the direct carbon substitution effect of using woodfuel instead of fossil fuel use, and a reduction in atmospheric pollutants (Lattimore et al., 2009) the management of land for woodfuel production is likely to rise.

The UK woodfuel sector is still considered as underdeveloped and growth is slower than excepted. Two reasons have been proposed for slower than expected growth; limited demand and fragmented supply base (Emmanuel-Yusuf et al., 2017). My personal communications with woodland managers identified that demand for woodfuel is now overtaking the demand for other products such as woodchip board in the construction industry (at least in the south-west of England).

In 2007 the world's woodfuel production was 1.89 billion m^3, equating to 53% of the world's total roundwood (wood in its natural state as felled) production (FAO, 2010). Although the climate change mitigation benefits of extracting trees (carbon sinks) from woodlands by means of machinery (emitting carbon dioxide) has been questioned (Luck et al., 2014) the use of woodfuel to generate electricity in combination with other renewables is of benefit to biodiversity as a whole to counter anthropogenic-induced climate warming and associated extreme weather events (Zickfeld et al., 2017). It may also be economically better as fossil fuel prices increase (Weatherall, 2009). In the UK,

the 'Woodfuel Strategy for England' established government targets to bring an annual addition of 2 million tonnes of wood to the wood fuel market by 2020. This will be achieved by reverting the UK's estimated 47% of abandoned or under-managed woodland into production (FC, 2007; FC, 2015). As it is unclear how this will affect woodland dependent species the possible benefits may not outweigh any potential biodiversity degradation. This may, however, not be the most efficient way to meet government targets. Increasing plantation woodland and directly using the extracted timber for woodfuel, or even utilising woodfuel as a by-product of good silviculture practice may yield greater return (Weatherall, 2009).

Two problems specific to countries such as the UK are limited woodland cover (EE, 2015), and the exaggerated potential negative impact to wildlife because woodland cover has considerable value to wildlife due to its relative scarcity within the landscape; a characteristic that influences biodiversity regardless of woodland age, structure or species composition (Fuentes-Montemayor et al., 2013).

1.3 Conservation ecology of woodland-dwelling bats

Bats account for 30% of the UK's and 20% of the world's mammal species (Mickleburgh et al., 2002; Altringham, 2003; Dietz and Kiefer, 2016). In Europe, there are 35 bat species (Dietz and Kiefer, 2016). Seventeen of these species are resident in the United Kingdom (Dietz and Kiefer, 2016) and all feed almost exclusively on arthropods, mainly insects (Altringham, 2003). All European bats use woodland to some extent with species such as *Barbastella barbastellus* (Schreber, 1774) considered woodland specialists (see chapter 3).

Worldwide deforestation has resulted in many bat species suffering severe population declines (Mickleburgh et al., 2002). Globally, the ecological and behavioural needs of woodland bats and how the management of woodlands influences the ability of a woodland to provide these needs has become the focus of research in recent years (Lacki et al., 2007; Russo et al., 2016).

Tree roost selection and spatial movements between tree roosts have received the most attention from researchers with agreed commonalities in the characteristics selected by bats across different woodland biome types (Lacki and Baker, 2003; Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015a; Naďo and Kaňuch, 2015). There remains some disagreement between studies, and fundamental unanswered questions include how many tree roosts are needed to maintain a colony, or population of tree-dwelling bats? Current estimates are based on roost removal simulation modelling for a single species (*Myotis sodalist*; Silvis et al., 2014). Our ability to measure woodland characteristics to a resolution required to understand selection at different scales impairs our ability to fully understand selection, although emerging remote technologies such as light detection and ranging (LiDAR) imagery is suitable (Froidevaux et al., 2016) and has been used effectively in my research to provide a new contribution to knowledge of roost site selection by bats (chapter 3). Wider landscape characteristics such as woodland patch size and connectivity affects the relative abundance of bats, and differences between the sexes are evident (Fuentes-Montemayor et al., 2013; Lintott et al., 2014a).

The capture of bats aided by acoustical lures and telemetry (and GPS for larger bats) has been fundamentally important in allowing researchers to locate and study woodland-dwelling bats (Russo et al., 2004; Zeale et al., 2012; Borkin and Parsons, 2014; Lintott et al., 2014b; Kirkpatrick et al., 2017). The behaviour of bats being radio tracked is mostly inferred from subtle changes in the emitted signal, although in combination with ultrasonic detectors researchers are able to assess activity levels, allowing identification of important areas within woodlands. It is possible to directly estimate feeding rates by recording terminal buzzes (typically emitted when prey are captured (Britton and Jones, 1999)), which has proven useful at areas with concentrated bat activity such as street lights (Rowse et al., 2015) but which has low efficacy in woodlands due to low echolocation call to feeding buzz ratios (Froidevaux et al., 2016). Inferring woodland suitability by bats through remote detection of their echolocation calls is valuable, but as foraging and commuting behaviour cannot always be separated, conclusions may be misleading. For example, inferring that riparian

woodland around rivers is good foraging habitat may be erroneous if such habitat is in fact used as commuting corridors (Lacki et al., 2007). Bats do appear to be more active in some areas of woodland than others (Ford et al., 2006; Froidevaux et al., 2016), presumably due to structural attributes, prey abundance or a combination of both (i.e. prey presence and the ability to catch that prey). In combination, radio telemetry study and acoustic monitoring provides more balanced conclusions when trying to infer woodland suitability for bats as they identify both habitat selection and a measure of use within that habitat (e.g. level of activity as used in this thesis).

1.4 Morphology and diet of woodland-dwelling bats

The opportunities that bats receive from woodlands is greatly influenced by their evolved wing morphology and echolocation traits. The size and shape of a bat's wing determines manoeuvrability, which affects where a bat will hunt for prey (Lacki et al., 2007). Wing loading has shown to be suitable as a proxy for predicting habitat use by bats (Patriquin and Barclay, 2003). A bat with low wing-loading is relatively manoeuvrable (i.e. can turn in a small volume of space) and is able exploit woodland interiors to capture prey (either by gleaning or in flight). Conversely a bat with high wing-loading is less manoeuvrable and needs to remain in relatively fast flight to stay volant (Norberg and Rayner, 1987). Echolocating bats orientate by using evolved echolocation components, such as the ratio of constant frequency to modulated frequencies that are influenced by the perceptual challenges of their environment (Jones and Holderied, 2007). A bat exploiting densely cluttered environments will have echolocation characteristics for effective spatial orientation to overcome 'clutter' echoes from surrounding vegetation (Schnitzler et al., 2003) and to identify and capture prey items. Such characteristics can include short calls (so that outgoing calls do not overlap with echoes from nearby objects) and the use of broadband signals (for localization of targets) (Jones and Holderied, 2007).

Eco-morphological traits are species-specific and relate to a bat's habitat niche (Lacki et al., 2007). As such, inferences have been successfully used to identify commonalties in how bats with similar eco-morphological traits respond to habitat structure (Froidevaux et al., 2016). Indeed, the use of guilds (defined as a group of species that exploit the same class of environmental resources in a similar way (Root, 1967)), such as echolocation range, wing loading and overall foraging strategy in bats (Denzinger and Schnitzler, 2013) provides inferences beyond predicting the behaviour of single species (Klingbeil and Willig, 2009). When assessing whether woodland structure influences bat activity, recognising guilds that consist of short-range, mid-range and long-range echolocators is appropriate (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2016), although inferences on responses to environmental and biological shifts should be explored at a species level when possible (Patriquin and Barclay, 2003; Obrist et al., 2011; Cistrone et al., 2015).

Dietary studies of animals that are difficult to directly observe feeding have improved with the advancement of molecular extraction and sequencing of fragmented DNA strands obtained from faecal pellets (King et al., 2008). The diets of many animal taxa have been identified through a molecular approach, including the feeding habits of marine species (Parsons et al., 2005; Braley et al., 2010), terrestrial herbivores (Soininen et al., 2009), and insectivores (Salinas-Ramos et al., 2015). The development of primers (short nucleic acid sequences that provide a start and end points for DNA synthesis) (Clare et al., 2009; Zeale et al., 2011), efficacy testing of these primers (Clarke et al., 2014), and ongoing technical refinement (Salinas-Ramos et al., 2015) is allowing researchers to identify consumed prey within bat faeces more often to species resolution (Razgour et al., 2011; Hope et al., 2014). These technical advancements improve on what was possible with non-molecular techniques (e.g. identification of prey parts by using microscopes (Rydell et al., 1996)).

Until relatively recently the mastication and digestion of prey by insectivorous bats, coupled with low morphological disparity among related insects, restricted investigation of diet through faecal analysis. However, by targeting short barcode fragments (157 bp) within mitochondrial DNA, insect

DNA can be amplified (Zeale et al., 2011) and importantly these short DNA fragments have enough sequence divergence to deliver species resolution. Barcode libraries such as the Barcode of Life Database (BOLD) (Ratnasingham and Hebert, 2007) are populated with token sequences to give confident identification hits. The barcode libraries for UK insect species (particularly moths) are comprehensive, and although there are some limitations such as taxa biases (see chapter 4 for more detail) that need to be refined, our ability to identify the diet of an animal through extracting prey DNA from their faeces is impressive. The application of these methods to understanding the prey resources exploited by forest-living bats has great potential, and can add value to studies of habitat use.

It is important to consider how woodland characteristics influence the distributions of insects known to be consumed by bats. Taking moths as an example, we know that as a group their richness and abundance is increased in mature broadleaved woodland with relatively high frequency of dead trees, and that we see further increases as the amount of woodland edge decreases in these woodlands (Lintott et al., 2014c). Diurnal lepidoptera appear to benefit from management presumably as the removal of trees provides a more open canopy and increased sunlight to the understorey (Taylor et al., 2013). Observed long-term population trends in common lepidopteran species indicates that seasonal temperature and precipitation are the drivers of distributions rather than local woodland characteristics such as woodland size, type or management (Fox et al., 2013).

1.5 Forestry and bat conservation

The conflict between forestry and conserving protected species can be contentious (Starr et al., 2011; Michalak, 2016; Nelson, 2018). In the UK, a forestry industry task force highlighted an urgent need for better evidence on which to base the regulations surrounding wildlife (Starr et al., 2011). Their concern was that wildlife regulations were deterring active woodland management; an example provided was the reluctance to remove conifer species on ancient woodland sites as the

burden associated with surveying each tree for potential bat resting places was too high but removing trees without surveying may result in an offence and possible prosecution. Their solution to this is that more resources are needed to establish a sound evidence base for determining to what degree approved woodland management activities affect European Protected Species. The UK Government recognises the burden associated with evidence-cited regulations of wildlife in woodlands and assures action to continue to fund research (Defra, 2012). Despite recognised knowledge gaps, the UK Government continues to incentivise landowners to revert abandoned and under-managed woodland into management for biomass extraction (FC, 2007).

Given the complex lifestyles of bats and the difficulty in observing their behaviour (Patriquin and Barclay, 2003; Lacki et al., 2007), many elements of their ecology require further investigation. The study of bats in woodlands is particularly problematic due to limitations of survey equipment (e.g. difficulties of detecting species with faint echolocation calls) and the complex habitat structure inherent in woodland habitats. All bats are listed as European Protected Species in the Habitats Directive 92/43/EEC which affords protection to bats and their roosts, and species considered to be of particular conservation concern also feature on Annex II of the Directive which requires core areas of their habitat are managed to promote their ecological requirements through Natura 2000 ecological network of protected areas (EC, 2018). Many threatened bat species lack information regarding their distribution and ecological requirements placing significant constraints on the level of protection that can be provided through conservation measures. The concern raised by the forestry industry therefore appears valid and the influence of woodland management on bats is unclear.

Five key research objectives for the conservation of bats in European woodlands have been identified (Russo et al., 2016) and include (i) the detection of factors that influence the carrying capacity of bats in woodlands, (ii) explore changes in bat activity or fitness as a result of woodland management which could be achieved by monitoring managed woodland against unmanaged

woodland (Cistrone et al., 2015), (iii) select some bat species or groups (perhaps determined by echolocation call guilds; Froidevaux et al., 2016) whose reactions might summarise responses to forestry by a wide range of taxa in the bat community, (iv) improve woodland areas by encouraging habitat and woodland characteristics preferred by woodland-dwelling species, and (v) aim to fill a current lack of understanding of how bats respond to woodland change over time using long-term longitudinal studies to monitor bat population trends after logging (Law et al., 2015).

Long-term longitudinal studies in slow-growing habitat such as broadleaved woodland is difficult and although studies are ongoing (summarised in Law et al. (2015)), informative results will take time to obtain. In addition, conclusions of these studies are likely to be affected by (1) changes in management over time as a result of economic shifts (e.g. growth in the biomass market encouraging reversion of under-managed woodland to management), (2) political motivations (e.g. selling off publicly owned woodland for short-term benefit during times of austerity (England's forest sell-off; https://www.theguardian.com/environment/england-forest-sell-off)), or (3) as a consequence of disease outbreaks such as that identified by the Polish government to justify increasing logging to counteract a European spruce bark beetle outbreak in the UNESCO Białowieża primeval forest (Michalak, 2016). I believe using a chronosequence approach (i.e. by using snap shots of similar woodland types at different stages of temporal development) is the best method in the absence of long-term study and removes the potential for future changes in exploitation confounding meaningful conclusions (see chapter 2 for more detail).

1.6 Protecting biodiversity through opt-in sustainable forestry certification

Smith (2017) argues that the characteristics that form in ancient woodland are well known and these characteristics can be achieved through managing young woodland to facilitate natural succession; Smith (2017) refers to this approach as 'facsimile ancient woodland'. The exact same argument can

be made for bats that use woodlands by first identifying the characteristics that facilitate bat use, and then managing woodland habitat to encourage the development of those characteristics.

In recent years UK forestry has become a good example of providing ecosystem services, particularly timber and recreation, whilst attempting to protect, maintain and enhance biodiversity. The United Kingdom Forestry Standard (UKFS) was first published in 1998, is now in its fourth revision, and is used to assess management operations and activities that promote the sustainability of UK woodlands (FC, 2017). The guidelines set out by the UKFS are divided between legal requirements and good forestry practice requirements at international and European levels. These form the basis for the independent UK Woodland Assurance Standard (UKWAS), which is used as a voluntary independent certification (UKWAS, 2017). The UKWAS certification is given to woodlands (or woodland management units) that can be demonstrated as sustainably managed. Section 2 of the certification encourages the restructuring of even-aged woodland stands to provide an appropriately diverse mosaic of species, sizes, ages, spatial scales, and regeneration cycles (UKWAS, 2017). Section 6 of the certification is concerned with the conservation of biodiversity and requires applicants to take steps to ensure a woodland is managed with enhancement of biodiversity as an objective by (i) creating permanently wooded areas in which the selected management type will benefit biodiversity, and (ii) providing both standing and fallen dead trees (UKWAS, 2017). Research that investigates the value of these recommendations is of great importance to bat conservation.

UK forestry has traditionally used clear fell silviculture (the process of growing, harvesting and regenerating a woodland or forest) (Mason et al., 1999) although continuous cover forestry (the maintenance of a forest canopy during the regeneration phase with a consequent presumption against clear felling in favour of alternative silvicultural systems) has increased, likely encouraged by the need to meet sustainable certification because it is seen as more sympathetic to biodiversity. Continuous cover forestry can be achieved at a similar economic cost than traditional clear fell and replanting (Davies and Kerr, 2011). I believe, when other factors allow (e.g. windthrow hazard), the

extraction of timber from UK woodlands and other European countries will be increasingly achieved through continuous cover forestry practice such as selective thinning (see chapter 2 for more detail). Research that targets how wildlife responds to selective thinning is therefore the most appropriate target with wide reaching applicability across Europe.

1.7 Research aims and thesis outline

Despite woodland being one of the most important habitats for bats, our understanding of how woodland characteristics relates to bat abundance and diversity remains limited; which is justifiable given the inherent complexity of woodland habitat and difficulties associated with researching nocturnal flying animals. Forestry standard certification is driving forward a better way to manage woodlands in the UK but the guidance provided to forestry practitioners is limited by the lack of an evidence base for what makes a woodland suitable for bats.

I use an integrated approach combining traditional and emerging technologies to provide an original contribution to scientific knowledge. First, I investigate how bat activity and diversity are affected by forestry practices in UK broadleaved woodland, and identify the woodland characteristics that best explain the level of bat activity and abundance of insects in woodlands. Second, to further explore the ecological requirements of a woodland-dwelling bat, I investigate roost selection by *B. barbastellus* at different spatial scales. Third, I investigate foraging habitat selection and the diet of *B. barbastellus*, and the habitat requirements of their consumed prey. Lastly, I combine group and species results to provide practical guidance to foresters and conservation managers that will improve woodlands for bats.

In chapter two I test the hypothesis that woodland management benefits bats and their insect prey by measuring the richness and activity of bats and the richness and biomass of their potential insect prey in managed (selective thinning forestry) and unmanaged (minimal intervention, management prohibited and underutilised) broadleaved woodlands. I identify important woodland characteristics

that most influence bats and insects, and explore the effect of time since management on bats and insects using a chronosequence approach.

In chapter three I test the hypothesis that roost selection by bats is random at a range of spatial scales by radio tracking *B. barbastellus* to tree roosts and measuring roost site characteristics using a combination of ground-based field surveys and airborne light detection and ranging (LiDAR) imagery, and compare roost characteristics with those of random trees to determine if roost selection occurs.

In chapter four I investigate the ranging behaviour and habitat selection of *B. barbastellus* by radio tracking individuals to foraging sites and I examine habitat selection using compositional analyses. I then compare these findings with the habitat requirements of their prey by extracting and sequencing insect DNA from *B. barbastellus* faecal pellets using second generation high-throughput sequencing and categorise prey by their habitat needs and conservation status.

In chapter five I consider the conclusions from chapters two, three and four alongside existing literature and provide guidance for improving woodlands for woodland-dwelling bats and their insect prey.

CHAPTER 2

The effects of woodland management by continuous cover selective thinning on bats and their insect prey

Abstract

Woodland is an important natural resource. When sustainably managed, woodland can provide carbon lean fuel for electricity and heating. Several bat species rely on woodland for roosting and foraging. A global reduction in woodland cover has resulted in historic declines and fragmented bat populations. The influence of woodland management on bat activity and consequences for populations is unclear.

I investigated the richness and activity of bats and the richness and biomass of their insect prey in managed (continuous cover intermediate to heavy selective thinning forestry) and unmanaged (minimal intervention, management prohibited and underutilised) broadleaved woodlands (*n* = 27 pairs) in England and Wales between 2014 and 2016, and explored the influence of time since last thinning using a chronosequence approach. Bats were sampled by capture methods and by acoustic monitoring. Insects were sampled by using light traps. Sixteen woodland characteristics were measured to investigate whether management influenced woodland characteristics, and to assess the relative importance of these characteristics to bats and their prey.

Woodland thinning significantly altered five of the measured woodland characteristics (amount of tree cavities and number of standing dead trees, basal area, below-canopy vegetation clutter and temperature). Bat species richness and activity were significantly greater in managed woodlands. Commonalities in bat responses to woodland characteristics included increased activity in response to (i) light levels, (ii) the amount of standing dead trees and (iii) the number of available tree cavities. Insect abundance was not affected by management but increased when below-canopy vegetation clutter increased, and decreased as night temperature increased. Bats and insects had contrasting non-linear temporal responses to time since last thinning with bat activity reducing, and insect numbers peaking in early stage successional woodland.

Common and adaptable edge foraging species of bats (*Pipistrellus pipistrellus* and *P. pygmaeus*) responded positively to management presumably by taking advantage of less cluttered woodland

interiors. Bats that have retained a preference for roosting in trees (*Barbastella barbastellus* and *Nyctalus noctula*) showed higher levels of activity in unmanaged woodland that provided more roosting opportunities. Standing dead trees were more than three times more abundant in unmanaged woodland than in managed woodland, and there were more than five times the number of available tree cavities in unmanaged woodland. The activity of woodland interior foragers (*Plecotus auritus*) was greater in unmanaged woodland and were unaffected by vegetation clutter.

A minimal intervention management approach (no systematic felling or planting of trees) is the most suitable action for bat conservation in woodlands, although sustainably thinned woodlands could be greatly improved as bat habitats by (1) retaining more standing deadwood and trees with cavities during thinning operations, (2) opening the upper canopy to allow light to penetrate the woodland interior, and (3) reducing below-canopy vegetation clutter.

2.1 Introduction

Woodlands are important wildlife habitats, absorb carbon dioxide, pollutants and greenhouse gases, and release oxygen. Woodlands mitigate climate change in three ways; carbon sequestration via net photosynthesis in growing trees, carbon storage in the ecosystem (especially soils) and carbon substitution (FC, 2017), indirectly from using timber rather than higher carbon footprint materials like concrete or steel, or directly when woodfuel is used instead of fossil fuels for heating and electricity. Reducing our reliance on fossil fuels and obtaining energy independence are major drivers for a global increase in biomass commodity trading (WEC, 2016). In 2016 biomass accounted for 10% of global energy supply (WEC, 2016).

Governments recognise the economic and renewable energy benefits of wood-derived products and are encouraging landowners to revert abandoned and under-managed woodlands back into sustainable management (FC, 2007; Renewables Obligation Order, 2015). The UK government continue to provide Countryside Stewardship grants through the Rural Development Programme for England (RDPE) and FY2 woodland infrastructure schemes which can provide a woodland owner the means to manage for wildlife conservation and to facilitate the production of woodfuel. Potentially half of all UK woodland is unmanaged (e.g. woodland that is not certified as sustainably managed) (PEFC, 2012) suggesting potential large-scale changes in woodland management are likely as private landowners are encouraged to manage woodlands by financial incentives.

Silvicultural interventions, such as thinning, affect the structural attributes of woodland. Stand age and composition, the amount and characteristics of tree cavities and canopy architecture are some of the attributes found to change with management interventions (Amar et al., 2010). Forestry practices therefore influence woodland bats by affecting roost availability (Russo et al., 2016) and foraging opportunities (Lacki et al., 2007). The hypothesised response of bats to the number of roosts available to them and how cluttered a woodland is are shown in Figure 2.1. Bats exhibit habitat specialisations which makes them vulnerable to anthropogenic changes including habitat

modification (Russo and Jones, 2015). Changes in woodland management affect the species richness and abundance of temperate bats (Smith and Gehrt, 2010; Dodd et al., 2013; Fuentes-Montemayor et al., 2013) with heterogeneous woodland structure benefitting some bat species (Patriquin and Barclay, 2003). Species-specific differences in how bats respond to woodland management are evident (Patriquin and Barclay, 2003; Smith and Gehrt, 2010). Russo et al. (2016) advocate the need for more applied research to further determine the impacts of woodland management on bats, and to identify the woodland characteristics influencing the carrying capacity of bats in woodlands at different scales.

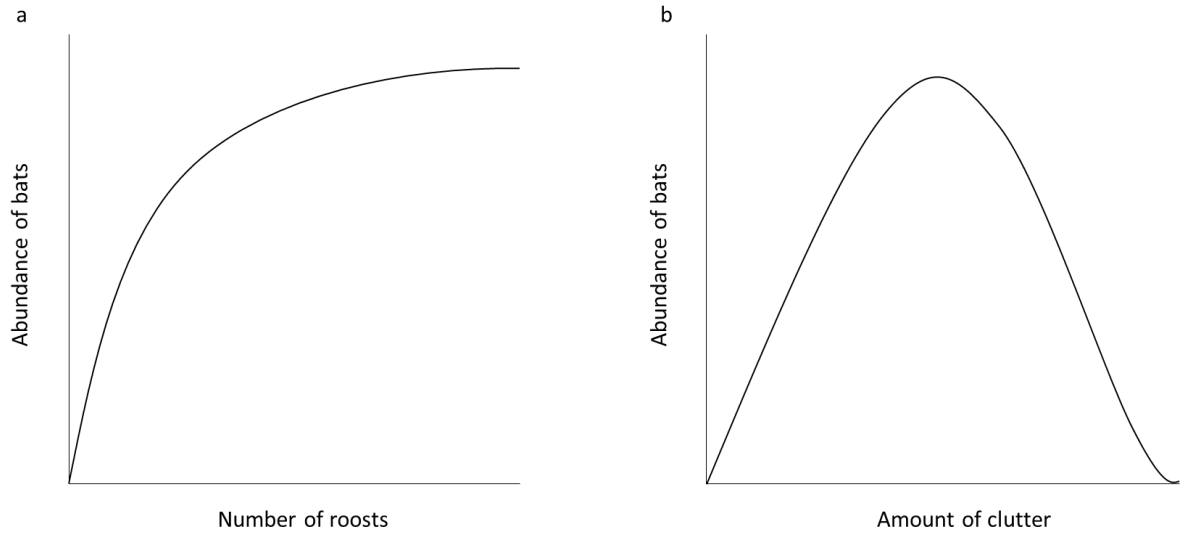


Figure 2.1 Adapted conceptual models illustrating hypothesised relationships between the abundance of bats and (a) the availability of roosts, and (b) the amount of clutter within woodland (Lacki et al., 2007). The number of roosts increases until a resource threshold is reached at which point increases in resources no longer lead to increases in the number of bats. When clutter is at low levels (such as in clear-cut woodland), there are low numbers of bats. The highest bat abundance is predicted at an intermediate level of clutter before then decreasing as clutter increases.

The process of thinning a woodland by continuous cover sustainable woodland management creates variation in structure, reduces vegetation clutter and creates canopy gaps allowing light to penetrate to ground level (FC, 2017). This type of active woodland management is typically viewed as beneficial to biodiversity (DEFRA, 2012; Peterken and Mountford, 2017) and many taxa associated with woodland respond positively to it (*Butterflies*; Taylor et al., 2013; s*aproxylic insects*; Horak et al., 2014; *bats*; Blakey et al., 2016). The hypothesis that thinning woodland is beneficial for temperate insectivorous bats needs rigorous scientific testing (Russo et al., 2016).

The management of sweet chestnut orchards (*Castanea sativa*) in Switzerland doubled bat species richness and significantly increased bat activity (Obrist et al., 2011). These increases were associated with changes in woodland structure rather than other characteristics such as prey availability. When pooling bat echolocation calls from several Italian bat species, Cistrone et al. (2015) found the amount of calls recorded increased in woodland undergoing thinning. In contrast, Patriquin and Barclay (2003) found that in the short-term thinning woodland has minimal effect on habitat use by bats in North America. These contrasting observations may be a result of differing thinning type (i.e. a first thinning in young dense trees or regular thinning in longer established woodland). Comparisons between studies may not be appropriate. Species-specific responses were documented in all these studies. Research into predator-prey relationships at the community level is advised when investigating the influence of management as prey availability and abundance may well be drivers of habitat suitability (Fuentes-Montemayor et al., 2012; Dodd et al., 2013). Despite an increased amount of research targeting the effect of forest thinning on North American bats (Patriquin and Barclay 2003; Loeb and Waldrop, 2008; Perry et al., 2008) there is a limited amount of research on the influence of woodland thinning on bats in Europe (*France*; Bouvet et al., 2016; *Germany*; Mehr et al., 2012 and Kortmann et al., 2017; *Italy*; Cistrone et al., 2015). As forestry prescriptions vary globally (Law et al., 2015) more European research is needed, especially in the UK where bringing woodlands back into management to contribute to woodfuel supply is a government objective (FC, 2007).

Here I test the hypotheses that woodland management by thinning increases the richness and activity of bats and the richness and biomass of their insect prey in managed (continuous cover forestry) broadleaved woodlands. Species specific responses are investigated. I identify important habitat characteristics that influence bat richness and activity, and the richness and biomass of their insect prey. Finally, I explore the relationship between time since last management and bat activity and the abundance of nocturnal insects using a chronosequence approach (i.e. by using snap shots of similar woodland types at different stages of temporal development).

2.2 Materials and methods

2.2.1 Study area and site selection

The study area covered large parts of southern England and Wales (Fig. 2.2). The landscape in these areas consists of a mosaic of fragmented habitats in an agricultural matrix with a temperate oceanic climate i.e. warm summers, mild winters and rain all year round (www.metoffice.gov.uk), which is typical for most of the UK and north-west Europe.

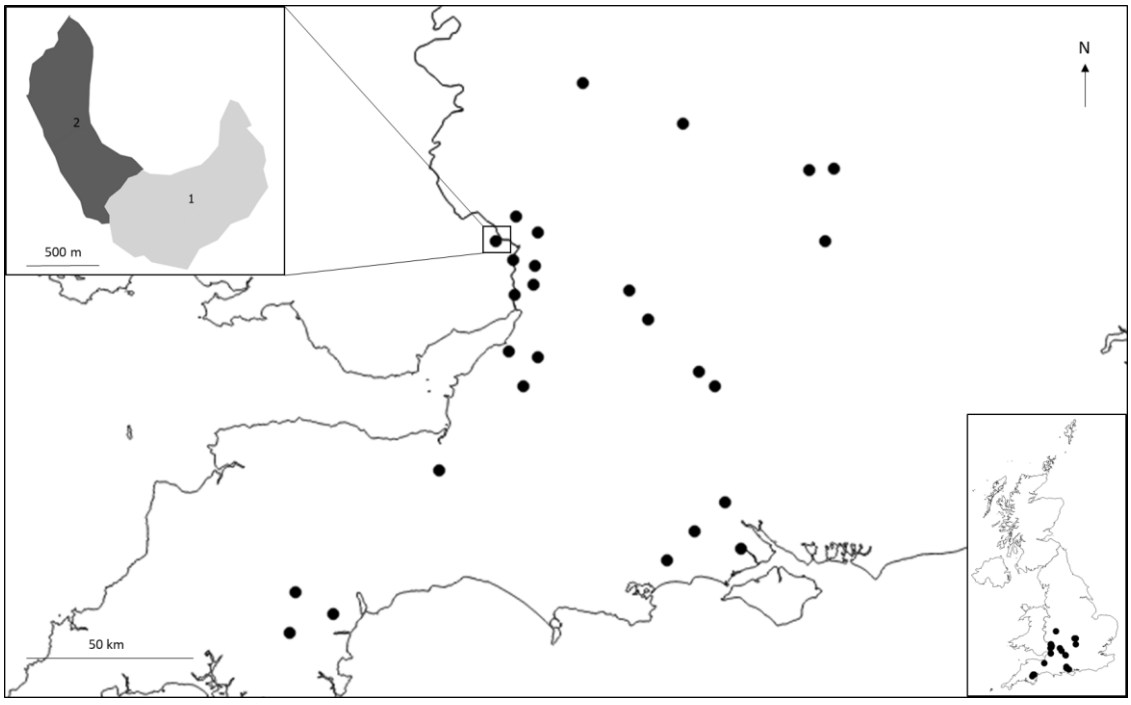


Figure 2.2 Location of woodland study sites in southern England and Wales surveyed between May and September in 2014 and 2016. Each study site (*n* = 27) consisted of two paired broadleaved woodland compartments, or stands within the same broadleaved woodland (*n* = 54) that were categorised as managed (1) or unmanaged (2). See section 2.2.1 for woodland management criteria. Points have been jittered.

All study sites (*n* = 27) were broadleaved woodland as categorised by the Forestry Commission Forestry Standard (FC, 2017), i.e. each site had a canopy cover of 20% or more with a minimum area of 0.5 ha with broadleaved trees accounting for at least 20% or more of the total tree cover, and conifer trees accounting for less than 10% of total tree cover. The minimum distance between sites was 1 km. The dominant tree species in all woodlands were either *Quercus* spp. or *Fagus sylvatica*. Each study site consisted of a matched pair of broadleaved woodland compartments or woodland stands within the same woodland. Each pair had the same dominant tree species. Power analysis of initial site surveys identified that 27 sites were suitable to confidently identify an effect on bat richness between the paired woodlands if present (see section 2.6 Supplementary material). Woodlands were categorised as either managed or unmanaged following Forestry Commission descriptions (FC, 2017) as follows:

1. Managed Broadleaved Woodland = woodland of any dominant broadleaved species. Woodlands were certified as sustainably managed (UKWAS, 2017). Management consisted of continuous cover forestry by selective thinning interventions on 10-15 year rotation. Low, crown or intermediate thinning ranging from intermediate to heavy (retention of 55% to 65% canopy cover) (Kerr and Haufe, 2011) was included. Clear-felling, small group felling or traditional woodland management such as coppicing were not included. Both upland and lowland woodlands were sampled.

2. Unmanaged Broadleaved Woodland = woodland of any dominant broadleaved species. These woodlands had not received any systematic management (as described above) for 20

years or more and included (i) abandoned (including neglected and under-utilised) woodland, (ii) research sites (woodlands used for research in which management was strictly forbidden with the exception of fencing to control for grazing), (iii) natural reserves (no felling or planting of trees (described in the UK woodland assurance standard; UKWAS, 2017)) and (iv) minimal intervention managed woodland (no systematic felling or planting of trees. Permitted management included fencing, control of exotic plant species and vertebrate pests, maintenance of paths and rides and safety work).

The selected minimum distance between pairs was 250 m (maximum distance = 1 km) to increase the likelihood of recording independent data while ensuring similar geographic and landscape characteristics. Independence has been considered as adequate for distances as low as 200 m for bats along river systems (Vaughan et al., 1996). This matched pairing protocol has been validated in research projects on bats and their prey around river systems (Vaughan et al., 1996; Scott et al., 2010), organic and conventional farmland (Wickramasinghe et al., 2003; Froidevaux et al., 2017), abandoned land (Obrist et al., 2011) and land included in agri-environmental schemes (Fuentes-Montemayor et al., 2011). Pairing in this way controls for environmental factors because comparisons are made on the same nights within pairs and, therefore, weather, geographic location, landscape barriers and variation in landscape characteristics are controlled.

2.2.2 Bat and insect sampling

All sampling took place between May and September in 2014 and 2016 during dry and warm nights (minimum temperature $\geq$ 5 °C) within the interior of each woodland at least 250 m from a woodland edge. Bats were sampled using complimentary acoustic and capture methods to maximise the chance of sampling all species and to allow inference of relative abundance (Lintott et al., 2014b). Insects were sampled using light traps only. Malaise traps and vegetation beating were trialled but proved either ineffective or had considerable bias (e.g. woodlands with high levels of shrub cover had more vegetation to beat than relatively shrub sparse woodlands).

Two Song Meter SM2BAT recorders were placed at each site (one unit simultaneously in each pair) (Wildlife Acoustics, Concord, USA) connected to an SMX-US ultrasonic microphone was mounted on a tree approximately 2 m from the ground. Uncompressed WAV recordings were taken and the settings on the detectors were: high pass filter 16 kHz (low pass filter was turned off); sample frequency 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 seconds; and trigger level 12 dB. Each detector was set to record bat echolocation calls from dusk until dawn for five to seven nights (the time a recorder was in situ was reduced to five nights after preliminary species accumulation curve analysis revealed species richness plateaued at five survey nights - see section 2.6 Supplementary material). To control for potential bias due to microphone characteristics a detector was randomly assigned to either a managed or unmanaged woodland. Each microphone and detector was checked for large variation in recording sensitivity between units prior to each field season using a semi-anechoic chamber with a microphone placed 1 m and at an angle of 45° from a speaker playing a series of high frequency sounds between 20 and 120 kHz. All detector systems used were comparable in sensitivity as determined by visual inspection of waveforms in BatSound (Pettersson Elektronik, Uppsala Science Park, Sweden). As acoustic sampling does not allow differentiation of individual bats, activity (number of bat passes) is used as a surrogate for bat abundance: activity is often positively correlated with relative abundance although can vary among species (Lintott et al., 2014b). A bat pass was defined as a series of at least two echolocation calls with pulse intervals < 1 s.

Pipistrellus spp. calls were separated from the data set using BatClassify (Scott and Altringham, 2014; www.bitbucket.org/chrisscott/batclassify); a freeware software package which has shown to perform well at correctly identifying species to genus level (Rydell et al., 2017). It was necessary to reduce the number of *Pipistrellus* spp. calls to a manageable amount prior to manual identification of sound files. Ten percent of *Pipistrellus* spp. calls were randomly selected and manually identified using BatSound 4.1.4 (Pettersson Elektronik, Uppsala Science Park, Sweden) to verify that the automatic identification by BatClassify was reliable. Bat calls were assigned to species or genus level

using call parameters in a guide to the echolocation calls of British bat species (Russ, 2012). Ambiguous *Pipistrellus* calls with frequencies at 51 kHz that could not be confidently assigned to species level were grouped as *Pipistrellus* spp. (Rachwald et al., 2016). *Myotis* spp. and *Plecotus* spp. could not be confidently identified to species level and so genus level identification was used. Multiple passes and/or species per file were identified following Rowse et al., (2016); their frequency was <1% of the full dataset and so were not considered in any analysis. For further consideration of different responses among bat guilds, echolocation range was used to categorise bats into guilds as short-range echolocators (SRE), mid-range echolocators (MRE) and long-range echolocators (LRE) (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2016).

Bats were captured by using 2.6 m and 6 m length 38 mm mesh 4 shelved bat mist nets (Avinet Inc., Portland, US) and 2 bank harp traps (Faunatech Austbat, Victoria, Australia) placed within each paired woodland for one night. Mist nets and harp traps were placed randomly close to the centre point of each woodland/woodland stand. Systematic placement to maximise bat catches was considered unsuitable and likely to result in bias as paired woodlands differed in characteristics (e.g. an unmanaged woodland may have a naturally formed commuting corridor whereas the paired managed woodland with evenly spaced trees may not). Apodemus acoustic lures (Apodemus field equipment, Mheer, Netherlands), broadcasting direct recordings of echolocation and social calls of all bats resident in the UK, were used to improve capture success (Hill and Greenaway, 2005; Lintott et al., 2014; Scott and Altringham, 2014). Calls were broadcast in sequence throughout a night on a set loop (i.e. 5 minutes of each different call) with 20 minute silent periods. Biometric data were taken for all captured bats including forearm length, weight, health, sex, age and reproductive state. All activity was conducted under Natural England licences 2014/SCI/0429 and 2016-20013-SCI-SCI-1.

Insects were sampled using portable generic Heath-type light traps (30 x 30 x 59 cm) with 6 W 12 V actinic bulbs (Sylvania, Wilmington, US) powered with 12 volt batteries, activated 15 minutes after sunset and turned off at dawn. One trap was placed in each woodland stand for one night. Light

traps were deployed on the same nights as bat surveys but positioned away from the acoustic bat detectors to avoid deterring or attracting bats (Froidevaux et al., 2018). Collected insects were euthanised and stored at -18°C. All samples were identified to family or species level using reference books (Skinner, 2009; Waring and Townsend, 2009; Sterling and Parsons, 2012) before being dried to a constant weight at 60°C for 48 hours (García-Barros, 2015) and weighed using a 0.1 mg readability Mettler-Toledo AE200 analytical balance (Mettler-Toledo LLC, Columbus, US).

2.2.3 Survey of woodland characteristics

To obtain comparable woodland characteristic variables, two 20 x 20 m quadrats were delimited within each woodland interior (*n* = 108). Measured characteristics included canopy architecture, diameter at breast height (DBH) and basal area per hectare, illuminance, number of tree cavities and amount of standing deadwood, temperature, tree height, and vegetation characteristics (Table 2.1).

Table 2.1 Survey methods in brief for habitat variables (*n* = 16) recorded from managed and unmanaged broadleaved woodland (*n* = 54).

Variable	Measurement
Basal area	Measure of total live standing wood within two 20 x 20 m plots[†]
Vegetation clutter (%)	% of clutter from the ground to 4 m in height at 36 points within two 20 x 20 m plots[††]
Ground flora richness	Count of the number of different species within four 2 x 2 m plots
Insect biomass (g)	Total dry weight of insects captured by light traps[†††]
Insect richness	Count of the number of different species captured by light traps
Light level (day) (lx)	Mean of Illuminance at 36 points within two 20 x 20 m plots
Light level (night) (lx)	Mean of Illuminance at 36 points within two 20 x 20 m plots
Number of cavities	Visual count of cavities from the ground within two 20 x 20 m plots
Shrub cover (%)	Visual estimate of vegetation cover at the shrub layer within two 20 x 20 m plots
Shrub richness	Count of the number of floral species at the shrub layer within two 20 x 20 m plots
Standing deadwood	Count of the number of standing dead trees within two 20 x 20 m plots
Temperature (day) (°C)	Measure of temperature using a thermometer at 36 points within two 20 x 20 m plots
Temperature (night) (°C)	Measure of temperature using a thermometer at 36 points within two 20 x 20 m plots
Time since management	Number of years since a woodland had received a management intervention
Tree height	Measure of the height of all trees within two 20 x 20 m plots using a clinometer
Tree height (SD)	Derived standard deviation of tree height

[†](Edwards, 1998), [††](Smith and Gehrt, 2010; Lintott et al., 2015a), [†††](García-Barros, 2015).

Each tree within a quadrat was (i) identified to species, (ii) classified as live or dead, (iii) measured for height using a clinometer (Invicta, Bicester, UK), and (iv) surveyed for the number of cavities present from the ground using 10 x magnification binoculars (Bresser-Hunter, Rhede, Germany). Eighteen evenly spaced points were established in each quadrat. Vegetation clutter was measured between 0-4 m in height at each point. Adapting a procedure used by Smith and Gehrt, (2010) and Lintott et al. (2015a) a four-metre pole with sixteen 0.25 m subsections marked on it was placed at each of the 18 points. Any vegetation touching a subsection was counted and summed to provide a measure of clutter from 0 - 100%. Illuminance and temperature was also measured at each of the 18 points during the day and one hour after sunset using a PeakTech 5025 lux meter (PeakTech, Ahrensburg, Germany) pointed directly upwards and a standard mercury thermometer. Shrub cover was assessed visually and categorised using the Domin scale (Rodwell, 2006). Floral richness was measured within two 2 x 2 m quadrats randomly placed within each of the 20 x 20 m quadrat.

To further explore the effect of time since last management on bats and insects I identified the last documented thinning intervention (management) for each woodland, using a combination of site management plans and by communicating with woodland managers.

2.2.4 Statistical analysis

2.2.4.1 Management and woodland characteristics

To explore whether woodland characteristics differed significantly between managed and unmanaged woodlands I undertook a series of univariate analyses on the variables. Paired t-tests were performed for parametric data while paired permutation tests (10,000 randomisations) were performed for non-parametric data.

To determine which woodland characteristics (not including time since management) in combination were different between managed and unmanaged woodlands, I performed a series of generalized linear mixed models (GLMMs) using maximum likelihood estimations with a binary response variable (managed or unmanaged) and a logit link function (lme4 package; R core team (Bates et al., 2015)).

Woodland pair was included as a random effect (Bolker et al., 2008). Multicollinearity was assessed prior to model building using Spearman's correlation tests and using a |r|>0.6 coefficient threshold. Insect richness and abundance were highly correlated. Insect richness was removed from analysis as I considered insect abundance as a more meaningful measure of prey availability given that quantity is probably more important than variety in the diet of bats, as is evidenced in chapter 3. To provide meaningful comparisons of effect size, data (x) were standardised by their means (μ) and standard deviation (σ) using the formula (x-μ)/σ. To identify the most parsimonious model that also explained the largest amount of variance, Akaike's Information Criterion (AIC) adjusted for small sample sizes (AICc) was used. A final model with only variables from the best fitting models using delta AICc (ΔI) ≤ 2 was selected.

2.2.4.2 Management, bats and their insect prey

To explore whether insect abundance differed significantly between managed and unmanaged woodlands I undertook a series of univariate analyses on the variables as described in section 2.2.4.1. To determine the influence of management type on response variables (i) bat richness and activity, (ii) echolocation guild activity, (iii) species or species group activity, and (iv) insect richness and biomass, and to explore which of the measured predictor variables contributed most to explaining any observed differences in response variables, I performed a series of Generalized Linear Mixed-Effect models (GLMMs; "lme4" package; Bates et al., 2015) with an appropriate distribution (i.e. Poisson or negative binomial family to handle overdispersion). Woodland pair was used as a random effect (Bolker et al., 2008). Multicollinearity was assessed prior to model building, as were any non-linear relationships between response variables (e.g. bat richness) and predictor variables (e.g. vegetation clutter). Predictor variables considered to have a non-linear relationship with response variables (time since management) were analysed separately (see section 2.2.4.3) and those deemed to be highly correlated to one or more other predictor variables (insect richness) using Spearman's correlation |r |>0.6 coefficient threshold were removed from analysis. To provide meaningful comparisons of effect size, data were standardised using mean and standard deviation

((x-μ)/σ). Comparisons of effect size and identification of the best models were performed as described in section 2.2.4.1. Marginal R^2 (variance explained by the fixed effects only) was applied for further consideration of model fit (Nakagawa and Schielzeth, 2013).

2.2.4.3 Time since management

The temporal association between bats and insects and time since last management was explored using a chronosequence approach (Johnson and Miyanishi, 2008). This is necessary in slowly changing habitats such as woodlands although I recognise that this snapshot approach may not always reflect succession in a dynamic woodland habitat because stochastic events such as a drought may result in unexpected climax species (Maron, 2005; Johnson and Miyanishi, 2008, Peterken and Mountford, 2017).

The predictor variable 'time since last management' was identified as having non-linear relationships with most response variables. To determine the influence of time since last systematic thinning intervention on (i) bat richness and activity, and (ii) insect richness and biomass, I performed a series of Generalized Linear Mixed-Effect Additive Models (GAMMs; "gamm4" package; Wood and Scheipl, 2017) with a smooth term and appropriate distribution (i.e. Poisson or negative binomial family to handle overdispersion). Woodland pair was included as a random effect. The predicted relationship between each response variable and time since management was plotted using GAMM model predictions (Wood and Scheipl, 2017).

All measurements of central tendency are presented as means +/- SDs unless otherwise stated. When applicable data were tested for normality using Shapiro-Wilk tests. All analyses were performed with R 3.3.2 (RStudio Team, 2015).

2.3 Results

2.3.1 Bat and insect sampling

Echolocation passes were recorded in managed (*n* = 22,914) and unmanaged woodland (*n* = 9,785) (Table 2.2). The common and widespread *P. pipistrellus* was detected most frequently and

dominated the bat assemblage with 62% of all verified bat calls, although elusive and rare woodland specialist bats including *Barbastella barbastellus* and *Rhinolophus ferrumequinum* were regularly recorded (Table 2.2). A total of 1,334 individual insects were captured between May 2014 and September 2016 within managed (n = 442) and unmanaged (n = 892) woodland. Most insects (97%) were moths. Insect biomass was significantly greater in unmanaged (median 0.3 ± 0.2 IQR grams) than in managed woodland (median 0.6 ± 0.3 IQR grams) (n = 54, perm, $p < 0.001$).

Table 2.2 Guild and species-specific bat activity (number of bat passes) in management and unmanaged broadleaved woodlands (n = 54) including the total number of sites each species or species group was recorded.

Taxa	Managed woodland	Unmanaged woodland	Total bat passes	% total passes	Number of sites
Pipistrellus pipistrellus[b]	16,369	3,997	20,366	62.28	27
Pipistrellus pygmaeus[b]	4,673	3,183	7,856	24.03	27
Myotis spp.[a†]	1,357	862	2,219	6.79	27
Nyctalus noctula[c]	183	721	904	2.76	22
Barbastella barbastellus[a]	46	558	604	1.85	14
Plecotus spp.[a††]	121	367	488	1.49	18
Eptesicus serotinus[c]	71	13	84	0.26	14
Rhinolophus hipposideros[a]	48	35	83	0.25	13
Nyctalus leisleri[c]	30	35	65	0.20	12
Rhinolophus ferrumequinum[a]	9	13	22	0.07	10
Pipistrellus spp.[b†††]	7	1	8	0.02	4
TOTAL	22,914	9,785	32,699	100	

[†] includes *M. alcathoe*, *M. bechsteinii*, *M. brandtii*, *M. daubentonii*, *M. mystacinus* and *M. nattereri* as identified from call features that could not be confidently catagorised to species level.

[††] includes *P. auritus* and potentially *P. austriacus* that could not be confidently identified to species level from call features.

[†††] includes *P. pipistrellus*, *P. pygmaeus*, and *P. nathusii* that could not be confidently identified to species level from call features.

[a] short-range echolocators; [b] mid-range echolocators; [c] long-range echolocators

A total of 17 adult bats were captured within managed and unmanaged broadleaved woodlands (*n* = 54) in 2014 and 2016 (between May and September), and included *Myotis brandtii*/*mystacinus* (*n* = 8); *Pipistrellus pipistrellus* (*n* = 4); *Plecotus auritus* (*n* = 2); *Pipistrellus pygmaeus* (*n* = 1); *Myotis daubentonii* (*n* = 1); and *Nyctalus noctula* (*n* = 1). Ten bats were captured in managed stands, seven in unmanaged stands. Capture data was considered insufficient to include in analysis.

2.3.2 Management and woodland characteristics

Univariate analysis identified seven of the 16 measured variables to be significantly different between managed and unmanaged woodlands (Table 2.3).

Table 2.3 Habitat variables recorded at managed and unmanaged woodland (*n* = 54). Values of central tendency for normally distributed variables (+) are presented as mean ± standard deviation, and for non-normally distributed variables (−) as median ± inter-quartile range. ns = not significant. ** $p < 0.01$ *** $p < 0.001$. ns = not significant.

Variable	Managed woodland	Unmanaged woodland	*p* value	Distribution
Basal area per hectare	16 ± 7	47 ± 24	***	+
Vegetation clutter (%)	22 ± 17	49 ± 23	***	+
Floral richness	5 ± 3	5 ± 3	ns	-
Invertebrate biomass (g)	0.3 ± 0.2	0.8 ± 0.6	***	-
Light level (day) (lx)	4069 ± 3496	1542 ± 2085	**	-
Light level (night) (lx)	0.0 ± 0.1	0.0 ± 0.0	ns	-
Management type	Categorical	Categorical	-	-
Number of tree cavities	3 ± 4	15 ± 13	***	-
SD tree height	2 ± 1	3 ± 1	ns	-
Shrub cover (%)	36 ± 38	36 ± 42	ns	-
Shrub richness	3 ± 1	2 ± 1	ns	-
Number of standing deadwood	0 ± 0	1 ± 1	***	-
Temperature (day) (°C)	21 ± 2	19 ± 2	ns	-
Temperature (night) (°C)	17 ± 1	16 ± 1	ns	-
Last thinning (years)	7 ± 5	44 ± 20	***	-
Tree height (m)	19 ± 2	18 ± 3	ns	+

The best model (ΔI ≤ 2) retained five variables and showed basal area per hectare ($p < 0.05$), number of cavities ($p < 0.05$), amount of vegetation clutter ($p < 0.01$) and number of standing dead trees ($p < 0.01$) were greater in unmanaged woodland than in managed woodland. In contrast, temperature was lower in unmanaged woodland than in managed woodland ($p < 0.05$) (Table 2.4).

Table 2.4 List of habitat variables from the best generalized linear mixed effects model (ΔI ≤ 2) including effect size, standard error, z statistic and *p* value. * $p < 0.05$ ** $p < 0.01$.

Response variable	Independent variable	Effect size	± SE	z	*p*
Management type	Basal area per hectare	4.1	1.4	2.9	**
	Number of tree cavities	2.3	0.9	2.4	*
	Vegetation clutter (%)	1.8	0.7	2.5	*
	Number of standing deadwood	2.2	0.9	2.4	**
	Temperature (day) (°C)	-1.1	0.5	-2.1	*

2.3.3 Management, bats and their insect prey

Management influenced most response variables (Table 2.5). Bat richness ($p < 0.05$), overall bat activity ($p < 0.01$), *P. pipistrellus* ($p < 0.001$) and *E. serontinus* ($p < 0.01$) activity were all positively influenced by management, and *P. pygmeaus* activity showed a positive trend. In contrast *B. barbastellus* activity ($p < 0.001$) was negatively influenced by active management, and *Plecotus* spp. and *N. noctula* showed negative trends. Only *Myotis* spp. activity was unaffected by management.

When modelling the influence of each woodland characteristic on bat activity seven variables were identified as important (Table 2.5). Light levels positively influenced bat richness ($p < 0.05$), overall bat activity ($p < 0.05$), *B. barbastellus* ($p < 0.001$), *P. pipistrellus* ($p < 0.05$) and *N. noctula* ($p < 0.05$) activity, and *P. pygmeaus* showed a positive trend suggesting these species select woodlands that allow solar radiation to penetrate through the upper woodland canopy which likely occurs when the

canopy is relatively open. *Myotis* spp., *Plecotus* spp. and *E. serotinus* activity were not influenced by light levels.

The number of standing dead trees positively influenced *B. barbastellus* ($p < 0.01$), *Myotis* spp. ($p < 0.05$) and *N. noctula* ($p < 0.01$) activity. Overall bat activity and *Plecotus* spp. activity showed a positive trend in relation to the number of standing dead trees and bat richness, *P. pipistrellus*, *P. pygmaeus* and *E. serotinus* activity were unaffected. The number of available cavities also positively influenced *B. barbastellus* ($p < 0.001$) and *P. pygmaeus* ($p < 0.05$) activity.

Shrub species richness positively influenced *B. barbastellus* ($p < 0.01$) and *Myotis* spp. ($p < 0.01$) activity. Surprisingly, temperature negatively influenced *P. pipistrellus* activity ($p < 0.05$). *P. pipistrellus* activity also showed a positive trend in relation to increasing tree height standard deviation. Only *Myotis* spp. activity was negatively influenced by clutter ($p < 0.001$).

When assessing the relationships among insect richness and biomass and woodland management type and characteristics, the best models found that insect abundance was unaffected by management type (Table 2.5). Vegetation clutter positively influenced insect richness ($p < 0.05$) and biomass ($p < 0.01$). Night temperature negatively influenced insect biomass ($p < 0.01$). Tree height negatively influenced biomass ($p > 0.05$) and shrub cover negatively influenced insect richness ($p < 0.01$).

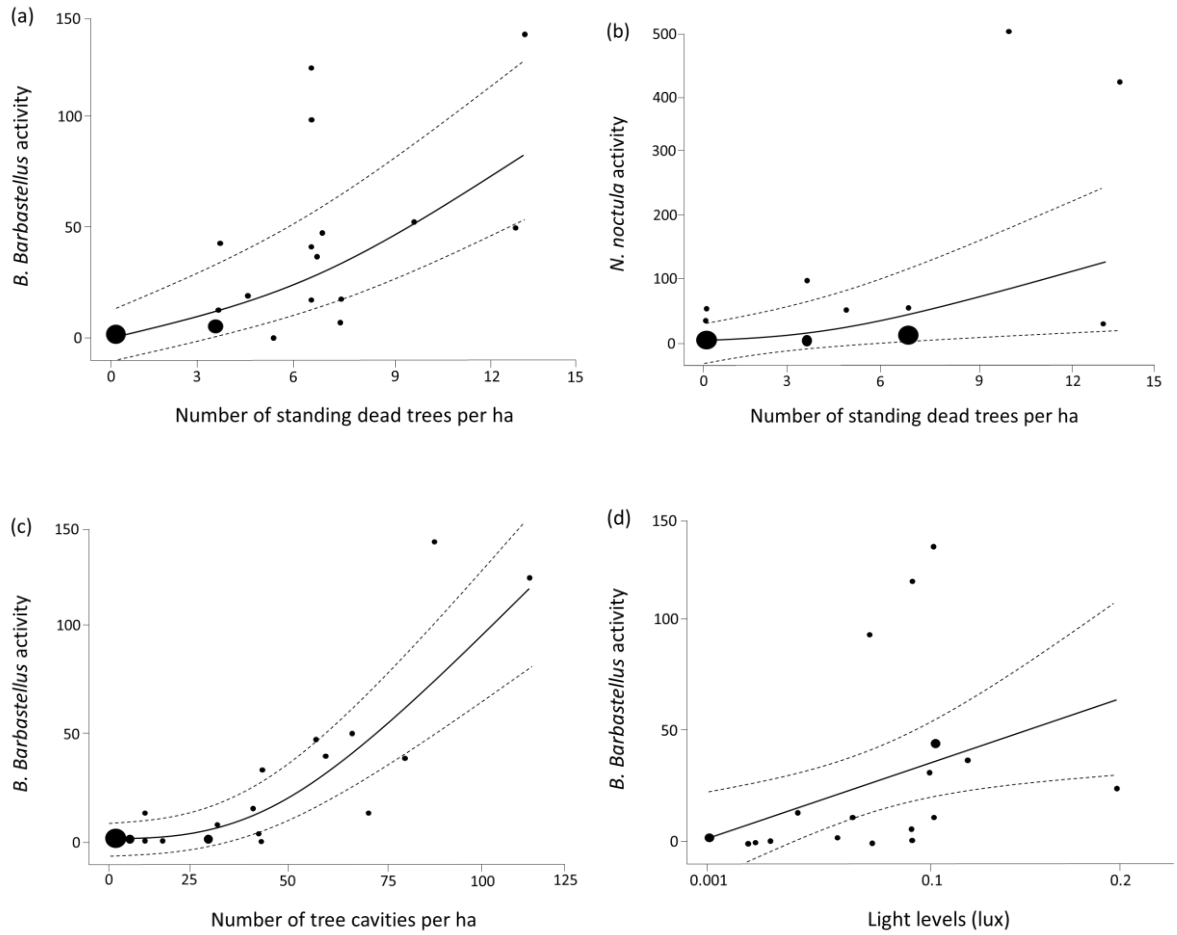
Table 2.5 List of habitat variables from the best generalized linear mixed effects models ($\Delta I \leq 2$) relating to management type and habitat characteristics for guild and species-specific bat activity and insect richness and biomass, including marginal R^2 (variance explained by the fixed effects only), effect size, standard error, z statistic and *p* value. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$. ns = not significant.

Response variable	Independent variable	Effect size	± SE	z	*p*
Bat richness	Basal area per hectare	0.2	0.1	2.2	*
Marginal R^2: 0.17	Light level (day) (lx)	0.2	0.1	2.2	*
	Management	0.3	0.2	2.2	*

Bat activity					
All bats	Deadwood	0.4	0.2	1.9	ns
Marginal R^2: 0.46	Light level (day) (lx)	0.5	0.2	2.2	*
	Management	1.2	0.4	2.9	**
B. barbastellus[a]	Cavity	0.6	0.1	4.7	***
Marginal R^2: 0.56	Deadwood	0.3	0.1	3.0	**
	Light level (night) (lx)	0.9	0.2	4.4	***
	Management	-1.3	0.3	-4.5	***
	Shrub richness	0.4	0.2	2.9	**
Myotis spp.[a]	Clutter (%)	-0.7	0.2	-4.1	***
Marginal R^2: 0.25	Deadwood	0.4	0.2	2.5	*
	Shrub richness	0.4	0.2	2.8	**
Plecotus spp.[a]	Deadwood	0.6	0.3	2.4	*
Marginal R^2: 0.53	Management	-0.8	0.5	-1.6	ns
P. pipistrellus[b]	Light level (day) (lx)	0.5	0.2	2.2	*
Marginal R^2: 0.31	Management	1.5	0.3	4.4	***
	SD tree height	0.3	0.2	1.8	ns
	Temperature (night) (°C)	-0.4	0.8	-2.3	*
P. pygmaeus[b]	Cavity	0.5	0.2	2.3	*
Marginal R^2: 0.38	Light level (day) (lx)	0.3	0.2	1.5	ns
	Management	0.8	0.5	1.6	ns
E. serotinus[c]	Management	1.9	0.6	2.8	**
Marginal R^2: 0.32					
N. noctula[c]	Deadwood	0.9	0.3	3.1	**
Marginal R^2: 0.29	Light level (day) (lx)	0.6	0.3	2.2	*
	Management	-0.2	0.5	-0.4	ns
Insect					
Biomass	Clutter (%)	0.2	0.1	2.9	**
Marginal R^2: 0.32	Temperature (night) (°C)	-0.2	0.1	-3.2	**
	Tree height (m)	-0.1	0.1	-2.4	*
Richness	Clutter (%)	0.2	0.1	2.0	*
Marginal R^2: 0.38	Shrub cover (%)	-0.3	0.1	-3.2	**

[a] short-range echolocators; [b] mid-range echolocators; [c] long-range echolocators. Lx = lux.

Prediction plots from the GLMMs show the biological significance of variables to each species or species group (Fig 2.3). *B. barbastellus* activity is predicted to increase by 50% when the number of standing dead trees per hectare increases from 0 to 15. The same increase in standing dead trees predicts only a modest increase in *N. noctula* activity. *B. barbastellus* activity is predicted to increase by 75% when the amount of available tree cavities in increases from 0 to 125 per hectare. An increase in light levels predicts increases in *B. barbastellus* activity but only modestly. A percentage of understorey vegetation clutter of 5% had the highest *Myotis* spp. activity with a predicted decrease of more than 50% as vegetation clutter increased by only 15%. A smaller increase in insect biomass is predicted as vegetation clutter increases.



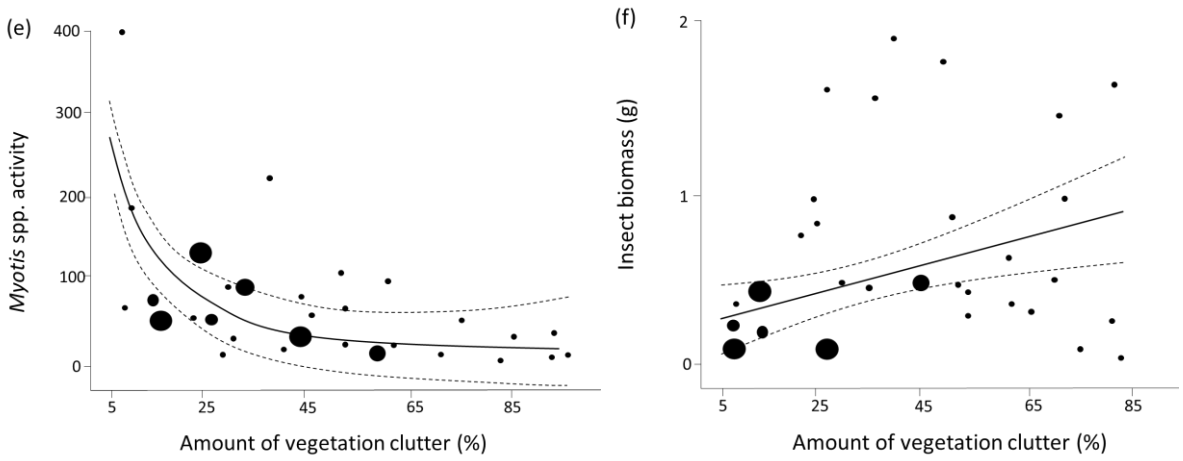


Figure 2.3 Predicted relationships from the best Generalized Linear Mixed Models (GLMMs) between highly significant variables (a) *B. barbastellus* activity; and (b) *N. noctula* activity and number of standing dead trees per hectare; (c) *B. barbastellus* activity and number of tree cavities per hectare; (d) *B. barbastellus* activity and light levels; and (e) *Myotis* spp. activity; and (f) Insect biomass activity and percentage of below canopy vegetation clutter. Model predictions are represented by the black solid lines with 95% confidence intervals indicated by dashed lines. Original data (number of passes recorded) are superimposed as black circles with diameter proportional to the number of sampling points where mean activity occurred. See table 2.5 for significance levels.

2.3.4 Time since last management

When assessing the influence of time since last management (from one to 65+ years of no systematic management as described in section 2.2), the best Generalized Additive Mixed Models (GAMMs) predicted non-linear relationships with some response variables. Bat richness ($p < 0.05$), overall bat activity, *P. pipistrellus* ($p < 0.001$), *P. pygmaeus* ($p < 0.01$), and *E. serotinus* ($p < 0.01$) activity levels initially started to reduce before increasing after 40 years of no management (Fig. 2.3). *B. barbastellus* ($p < 0.001$) and *Plecotus* spp. ($p < 0.001$) activity generally showed positive increases in activity after management (Fig. 2.4). Insect biomass ($p < 0.01$) and richness ($p < 0.01$) both showed to increase after management although richness then began to fall after peaking at 15 years to a minimum at 50 years (Fig. 2.5).

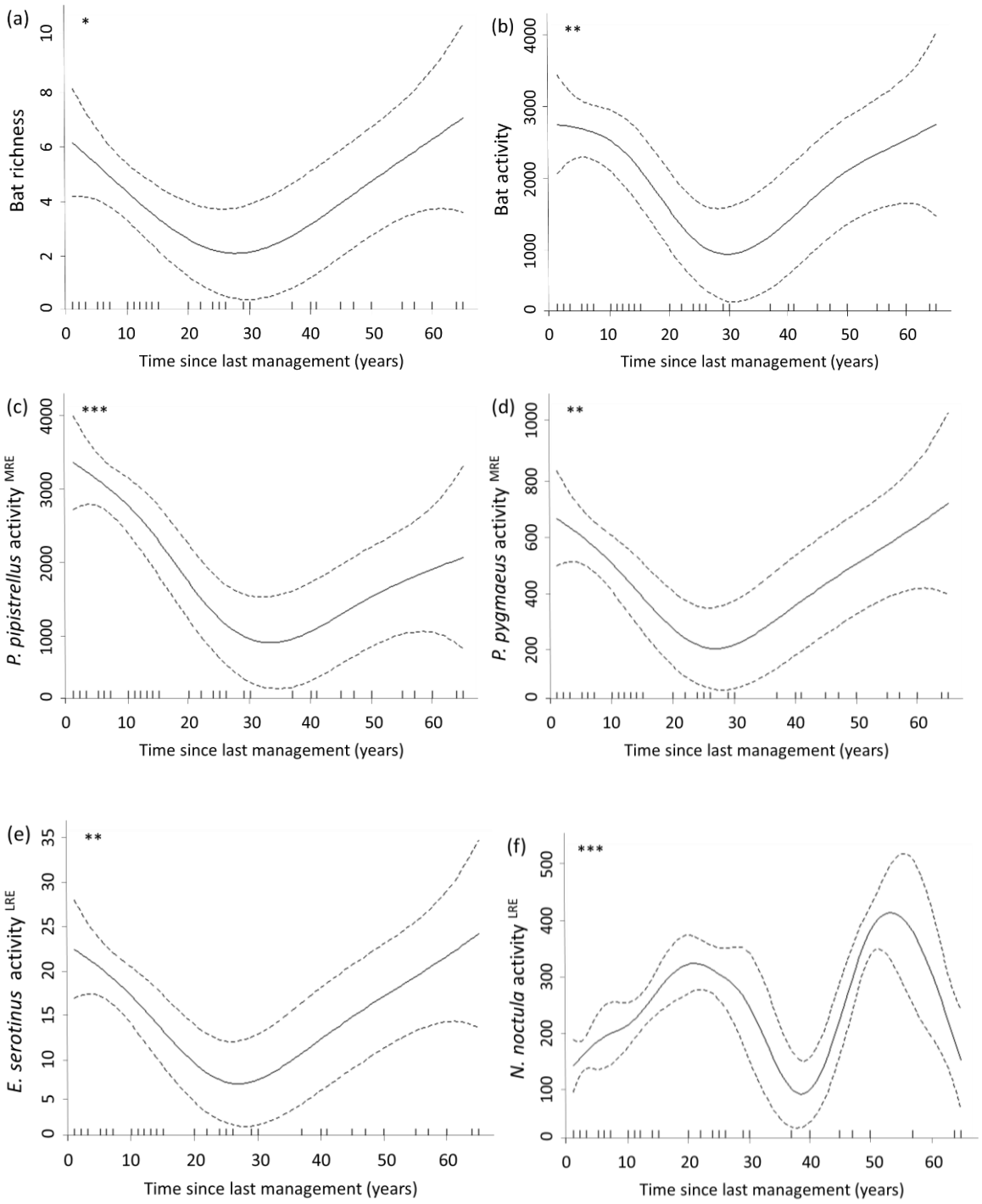


Figure 2.4 Predicted relationships from the best generalized additive mixed models (GAMM) between (a) bat richness; (b) bat activity; (c) *P. pipistrellus* activity; (d) *P. pygmaeus* activity; (e) *E. serotinus* activity; and (f) *N. noctula* activity and time since last systematic thinning intervention. Model predictions are represented by the black solid lines with 95% confidence intervals indicated by dashed lines. Significance values are taken from GAMMs. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$. MRE = mid-range echolocators, LRE = long-range echolocators.

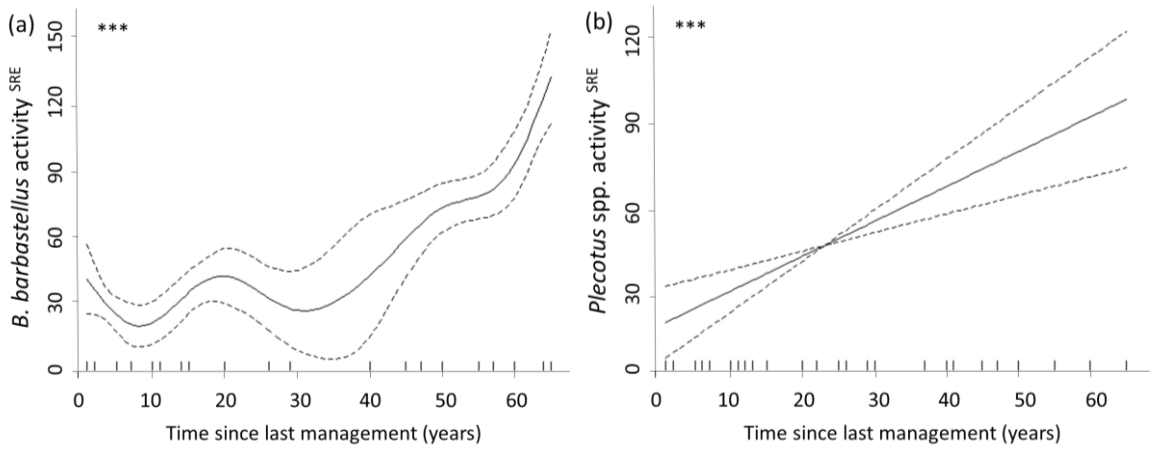


Figure 2.5 Predicted relationships from the best generalized additive mixed model (GAMM) between (a) *B. barbastellus*; (b) *P. auritus* activity and time since last systematic thinning intervention. Model predictions are represented by the black solid lines with 95% confidence intervals indicated by dashed lines. Significance values are taken from GAMMs. *** $p < 0.001$. SRE = short-range echolocators.

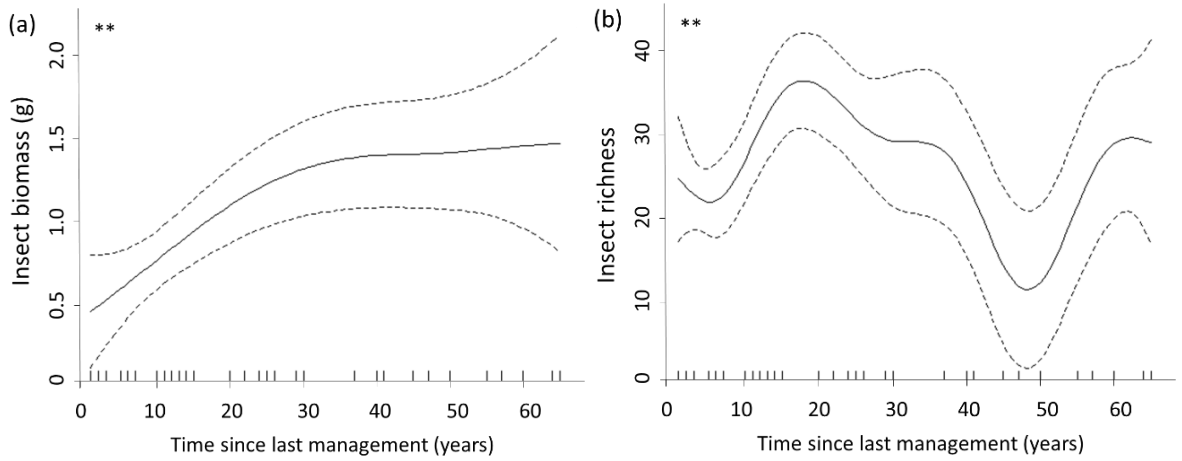


Figure 2.6 Predicted relationships from the best generalized additive mixed models (GAMMs) between (a) insect richness; and (b) insect biomass and time since last systematic thinning intervention. Model predictions are represented by the black solid lines with 95% confidence intervals indicated by dashed lines. Significance values are taken from GAMMs. ** $p < 0.01$.

2.4 Discussion

2.4.1 Influence of management on woodland characteristics

I found that thinning a woodland significantly influenced five habitat characteristics (Basal area per hectare, understorey vegetation clutter, number of standing dead trees and tree cavities, and temperature). These characteristics have been documented as important to woodland bats (Fuentes-Montemayor et al., 2013; Dodd et al., 2013; Smith and Gehrt, 2010).

Unmanaged woodland had a greater basal area per hectare and larger amount of understory vegetation clutter in comparison to managed woodland. Current thinning guidelines (Kerr and Haufe, 2011) would place the majority (67%) of these unmanaged woodlands as fully stocked and requiring a thinning intervention. All managed woodlands were below the basal area per hectare threshold that would trigger a management intervention. Although basal area is a suitable measurement to show the amount of standing wood volume it is not useful in indicating whether a woodland consists of many smaller trees or fewer larger trees; a characteristic that may influence suitability for bats and insects.

The number of standing dead trees per hectare was more than three times greater in unmanaged woodland than in managed woodland; and the number of cavities per hectare more than five times higher in unmanaged woodland. These differences suggest that management degraded the quality of woodland for bats by reducing roosting opportunity and limiting their ecological requirements for protection, sociality and reproduction (Kunz and Lumsden, 2003). This problem has been highlighted in holm oak (*Quercus ilex*) woodlands in which the density of trees with cavities was approximately 13 times higher in older woodland stands (>90 years) than in recently cut stands (<30 years) (Regnery et al., 2013).

The UK Woodland Assurance Standard (UKWAS) maintenance of biodiversity and ecological function guidelines for sustainable management state that at least 20m^3/ha of dead trees should be achieved within a woodland management area (UKWAS, 2017). Whether these dead trees are standing or

fallen is not distinguished, and the retention of cavities on trees is not specifically mentioned, presumably because dead trees are assumed to provide these features. A more suitable approach to assess the amount of dead trees needed for faunal biodiversity has been used in Australia by Webala et al. (2010) who used trees with cavities as a measure of roosting opportunity and found that Gould's long-eared bat, *Nyctophilus gouldi*, and the southern forest bat, *Vespadelus regulus*, preferred roosting in older forest that contained a much higher density of trees with cavities (16–32 trees/ha) than shelterwood creation and gap release sites (8–12 trees/ha).

Natural forests are structurally heterogeneous and include trees with a large variation in size (Bauhus et al., 2009). European woodlands that are managed have historically been even-aged stands (Russo et al., 2016). Current UK sustainable certification advises woodlands should achieve some variability in age structure, specifically encouraging restructuring even-age stands to include a diverse mosaic of species, sizes, ages, spatial scales and regeneration cycles (UKWAS, 2017). I found that woodland canopy heterogeneity (i.e. variation in canopy tree height), shrub richness and percentage of cover, and floral richness were comparable between managed and unmanaged woodlands. This highlights a positive outlook in UK forestry advancements for managing biodiversity, and *P. pipistrellus* activity was indeed positively influenced by canopy heterogeneity and *B. barbastellus* activity increased when the shrub layer diversity increased, which has also been observed for *Pipistrellus* spp. in Germany (Renner et al., 2018).

2.4.2 Influence of management on bats and their insect prey

I found that bat richness and overall activity was greater in managed woodlands suggesting it is possible to sustainably manage broadleaved woodland through thinning interventions as a commercial activity without reducing the presence and opportunity for temperate bat species. This positive response of bat richness to management has been observed in sweet chestnut orchards (*C. sativa*) in southern Switzerland (Obrist et al., 2011) and bat activity has shown to significantly increase in managed loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine forests in the US (Loeb

and Waldrop, 2008) and at some sites in Italian high forests (Cistrone et al., 2015). Bat richness and overall activity increased with light levels. An increase in light levels below the canopy suggests that managed woodland had a more open canopy thus allowing light to penetrate to the interior or had less clutter allowing more light to penetrate through the side.

The more abundant and adaptable *P. pipistrellus* (62% of all recorded calls) and to a lesser extent *P. pygmeaus* (24% of all recorded calls) strongly influenced the statistical output when all bats were grouped together. Suggesting that thinning a woodland will be positive to all bats is misleading. Habitat suitability studies for bats should be made at the species level when possible, or at least using guilds based on ecomorphology (Law et al., 2015) or echolocation call traits (Russo et al., 2016), as the evolved morphology and echolocation characteristics of bats varies by species as does their foraging and roosting behaviour.

2.4.2.1 Guild-specific responses

Guild-specific responses to thinning were evident. SRE bat activity was greater in unmanaged woodland and positively responded to the amount of standing dead trees and number of tree cavities available. The density of tree cavities and number of standing dead trees sufficient to support populations of woodland-dwelling bats are major knowledge gaps in bat conservation (Law et al., 2015; Russo et al., 2016) and my results further highlight the importance of filling these knowledge gaps for bat species adapted to living in the forest interior (i.e. SRE species).

MRE bat activity was greater in managed woodland and increased with light levels and canopy heterogeneity. These positive responses highlight the importance of a relatively open and structurally diverse canopy architecture. MRE bats often forage at habitat edges, and bats in this guild exploit the upper canopy of heterogeneous high forests, presumably to forage (Müller et al., 2013; Froidevaux et al., 2016).

LRE bats varied in their responses to management. The tree-dwelling *N. noctula* negatively responded to management and positively responded to the amount of standing dead trees and

increasing below-canopy light levels, showing that roosting opportunity and possibly ambient temperature (determined through solar radiation) at roosting sites are drivers for the presence of LRE tree-dwelling species. In contrast, *E. serotinus* (a species rarely found roosting in trees (Tink et al., 2014)) responded positively to management, suggesting that thinning interventions created a less cluttered environment for larger bats to exploit as foraging grounds, as observed in other relatively large temperate species such as *Eptesicus fuscus* (Cox et al., 2016) and open-space foraging bats in Germany (Jung et al., 2012).

Although grouping bats into guilds based on their echolocation traits allowed some inference about their collective responses to management and habitat characteristics, the relative importance of forest characteristics to each species within a group was variable and these species-specific differences should be considered.

2.4.2.2 Species-specific responses

B. barbastellus was recorded at 14 study sites and the activity of this species was consistently greater in unmanaged woodland. I did not record any calls at seven managed woodlands despite *B. barbastellus* echolocation calls being recorded in the paired unmanaged woodland. This agrees with research in beech forests in central Italy that captured both male and female *B. barbastellus* in managed and unmanaged forest, although more were captured in unmanaged forest (Russo et al., 2010). At a landscape scale, *B. barbastellus* is predicted to avoid production forests and favour dense areas of native woodland (Rebelo and Jones, 2010).

B. barbastellus activity was positively influenced by the number of available cavities, the amount of standing deadwood and increasing light levels. These habitat characteristics influence the amount and quality of roosting opportunities within woodland, which is the likely driver of woodland suitability for this species (Russo et al., 2004; Piraccini, 2016). Higher light levels are a proxy for canopy openness, and *B. barbastellus* activity levels have been observed higher in woodland with relatively open canopy compared to closed canopy woodland (Kortmann et al., 2017). Plant species

richness in the woodland shrub layer positively influenced activity. *B. barbastellus* presence has been associated with dense sub-canopy vegetation (Law et al., 2015) and although I found no influence of vegetation clutter on *B. barbastella* activity, (which would indicate a dense sub-canopy vegetation), the positive influence of shrub richness may not reflect the density (as considered by Law et al. (2015)) but the diversity of vegetation.

General guidelines for managing woodlands for *B. barbastellus* include encouraging (i) minimal intervention management, (ii) the retention of standing dead trees, (iii) the removal of invasive vegetation, (iv) control of overgrazing, (v) a humid environment and (vi) maintaining a closed canopy (Sylva, 2018). Guidelines i – iv may indeed improve woodland habitat for this species by ensuring standing dead trees are present in sufficient numbers (which has shown to be a driver of tree cavity formation - see chapter 3) and provide diversity within the shrub layer. My findings disagree with the recommendation that creating a closed canopy will be beneficial, and agrees with the findings of Kortmann et al. (2017) that *B. barbastellus* benefits from a relatively open canopy which is particularly true for individuals experiencing reproductive pressure such as lactating bats (Russo et al., 2007). I do recognise that a closed canopy encourages early emergence times for this species, which may allow longer nightly foraging periods, and as proposed by Russo et al. (2007) and further detailed in chapter 3, providing heterogenic canopy architecture with areas of open and closed canopy would be a suitable management approach.

Myotis bats were equally active in managed and unmanaged woodland. Their activity was positively influenced by the number of standing dead trees and a species diverse shrub layer. Only *Myotis* bats were affected by vegetation clutter, with significantly less activity in more clutter suggesting that their ability to deal with 'clutter' echoes from surrounding vegetation (Schnitzler et al., 2003) is limited. In contrast, the gleaning *Myotis nattereri* has shown to be positively influenced by dense understory clutter in woodland fragments in agricultural matrices (Fuentes-Montemayor et al., 2013). The difference between my findings and those of Fuentes-Montemayor et al. (2013) is

probably due to my data grouping bats that frequently glean prey from vegetation (e.g. *M. nattereri*) and bats that often hunt by aerial hawking (e.g. *M. mystacinus*) (Siemers and Swift, 2006). The relatively low explanatory power of the *Myotis* spp. model (R^2 = 0.25) further suggests that within-group diversity in wing morphology and echolocation traits resulted in conclusions that cannot be generalised across the genus. A higher rate of capture would have allowed a better understanding of species-specific responses.

Plecotus bat activity was greater in unmanaged woodland, and the quantity of standing dead trees positively influenced their activity. Although it was not possible to separate this group to species level (i.e. *P. auritus* or *P. austriacus*) acoustically, *P. auritus* was the only species captured and *P. austriacus* forages over unimproved grassland and roosts almost exclusively in manmade structures (Razgour, 2012). It is therefore highly likely all bats that I recorded were *P. auritus*. Thinning may be detrimental to interior hunting species such as *Plecotus auritus* by reducing clutter and presumably limiting the surfaces on which it can glean prey (Russo et al., 2016). Although the species responded negatively to management; vegetation clutter, shrub cover or species, floral richness and insect biomass were not identified as influencing activity, leaving the amount of standing dead trees as responsible for the observed increase in activity within unmanaged woodland.

P. pipistrellus activity was greater in managed woodland, and positively influenced by canopy heterogeneity and below-canopy light levels showing canopy architecture as the main driver. Canopy ruggedness increases *P. pipistrellus* activity (Froidevaux et al., 2016) and Müller et al. (2013) observed *Pipistrellus* spp. regularly foraging above the canopy in closed canopy mature woodland.

P. pygmaeus is a sympatric with *P. pipistrellus* (Jones and Van Parijs, 1993) and similarities in responses to management were evident with *P. pygmaeus* activity being greater in managed woodland and positively influenced by increasing light levels. *P. pygmaeus* activity was also positively influenced by the number of available cavities, suggesting that *P. pygmaeus* continues to rely on roosts within trees in addition to roosts within buildings unlike *P. pipistrellus* in which activity

was not influenced by cavity number. The relative abundance of *P. pygmaeus* in woodland has shown to decrease with proximity to urbanisation (Lintott et al., 2015a).

E. serotinus activity was greater in managed woodland. Activity was not influenced by any of the measured woodland characteristics. *E. serotinus* is a relatively large bat that roosts primarily in buildings and is rarely found in tree roosts (Tink et al., 2014). It is therefore likely the species was foraging which would explain why management was important as vegetation clutter was significantly reduced, allowing space for a relatively large bat to manoeuvre and capture prey.

N. noctula activity was greater in unmanaged woodland and positively influenced by the frequency of standing dead trees and light levels. Throughout Europe *N. noctula* has retained a preference for roosting in tree cavities (Ruczyński, 2006) and my results suggest that the availability of tree roosting opportunities (Ruczyński and Bogdanowicz, 2005) and canopy architecture, attributes that influence the temperature at these roosts, are important for the species.

2.4.2.3 Insect responses

Although univariate analysis found insect biomass was significantly greater in unmanaged woodland, linear modelling did not identify management type as affecting either insect biomass or richness. Insect richness and biomass was positively influenced by vegetation clutter, which was significantly higher in unmanaged woodland. Captured insects consisted mostly of Lepidoptera (97%), hence my findings suggest that moths benefit from substantial amounts of below-canopy vegetation clutter. Fuentes-Montemayor et al. (2013) found the same response to clutter by flies. Generally then, woodlands with dense understory vegetation have shown to be important habitats for insectivorous bat prey.

Abundant prey resources should be beneficial for bats and increase their activity; however if a bat is unable to capture prey by being hampered by vegetation clutter as found in understory foraging frugivorous species (Marciente et al., 2015), bats will not benefit from increased prey abundance, particularly when hunting mobile prey. Russo et al. (2004) found no association between insect prey

abundance and the activity of the moth specialist *B. barbastellus* in beech forests in Italy, suggesting that the richness or abundance of potential prey may not be a good measure of woodland suitability for bats. In agreement I found insect biomass did not influence bat richness or activity at any level, reinforcing the hypothesis that increasing prey abundance alone is not a key factor for bat conservation in woodland habitats (with the caveat that most of the insects that I caught were moths). A dense below-canopy vegetation clutter reduces the predation pressure on insects by aerial insectivores such as bats and birds, and may explain the increased abundance of insects at more cluttered sites although this may simply occur as more foliage provides more food for insect larvae (Root et al., 2017) or creates abundant micro-habitat and micro-climate (Merckx et al., 2012).

Insect biomass reduced as night temperatures increased. This was unexpected as moths are known to fly more often on warmer evenings (Hardwick, 1972; Lintott et al., 2014c). This reduction in biomass may be a chance finding in the data, or suggests other characteristics not measured are responsible for biomass. Although light intensity has been found to reduce nocturnal moth abundance when comparing relatively open coppiced broadleaved woodland with climax broadleaved woodland (Merckx et al., 2012) I found no evidence of this in the climax woodlands I surveyed, although vegetation clutter may well produce microhabitats with lower intensity light. In contrast to day-flying moths that typically derive body heat from the sun (heliothermic), nocturnal moths obtain body heat from muscular energy (myothermic) (Clench, 1966) which explains why the sampled insect richness and biomass did not increase with solar exposure as has been found with day-flying Lepidoptera (Merckx et al., 2012; Taylor et al., 2013). It is important to consider that within group strategies (i.e. diurnal or nocturnal behaviour) results in different selected woodland characteristics (e.g. a preference for open or closed woodland canopy) and may require separate conservation prescriptions.

2.4.3 Influence of time since last management on bats and their insect prey

When categorising each of the 54 woodlands by time since last management (as described in section 2.2.1) non-linear relationships between bats and insects, and woodland succession were evident. Bat richness and activity followed the same non-linear temporal relationship than those proposed by Lacki et al. (2007); richness and activity were initially high in relatively uncluttered woodland, followed by decreases in densely cluttered woodland, with later increases as natural succession was likely to reduce vegetation clutter. Indeed, if overgrazing is not a problem, a woodland has high levels of below-canopy vegetation clutter around 30 years of succession (Adams et al., 2009; Peterken and Mountford, 2017). The activity levels of LRE and MRE bats were at their lowest points at and around 30 years of no management. Any effect of below-canopy vegetation clutter on the activity levels of SRE bats was not obvious, with both *B. barbastellus* and *Plecotus* spp. activity increasing as time since management increased.

In contrast, the non-linear relationship between insect richness and biomass and time since last management started at a relatively low level, before increasing. Insect richness was predicted to peak at 20 years of management before decreasing. Fuentes-Montemayor et al. (2013) found a higher number of insects in densely cluttered broadleaved and mixed woodlands, supporting the hypothesis that insect richness may peak when clutter levels are highest during succession.

The relatively large woodland-foraging bat *E. serotinus* showed a clear reduction in activity from one year after management to 30 years after no management before increasing. This observed temporal relationship is most likely associated with canopy vegetation clutter and agrees with Adams et al., (2009) who observed higher bat activity levels along tracks (sparse to no ground vegetation) than away from tracks (more distinct understory trees and shrubs) regardless of guild (i.e. for both edge or open space foragers).

In contrast to other bat species *Plecotus* spp. and *B. barbastellus* were not negatively influenced during these early successional stage periods, instead showing a more linear increase in activity once

management had stopped. This shows that although these species are able to exploit abundant prey during early woodland succession stages they were not influenced by prey abundance. The level of activity for these two bat species continues to increase with time since last management, corresponding with observed increases in cavities in woodlands (Regnery et al., 2013), a likely causal explanation for my findings.

In disagreement with Patriquin and Barclay (2003) who consider that thinning woodland has minimal effect on habitat use by bats, I suggest that thinning has a profound influence on bats, as also suggested by Adams et al., (2009) and Obrist et al., (2011), which is best evidenced through the change in bat richness and overall activity over time since last thinning.

2.4.4 Commonalities in bat responses to woodland characteristics

Overall bat activity, and activity of more than half of all bat taxa increased in relation to the quantity of standing dead trees and the number of available tree cavities within a woodland, and no species or guild showed reduced activity in response to these features. In agreement with Kirkpatrick et al. (2017) who studied bats (mainly *Pipistrellus* spp.) in conifer plantations in Scotland and Russo et al. (2010) who found *B. barbastellus* presence in beech forests in Italy was best explained by the number of dead trees and tree cavity frequency, it is likely that roost availability rather than other features such as prey availability is the constraining factor affecting bat activity in many woodland habitats. Indeed, insect abundance (albeit mainly moths) did not influence bat activity at any level (i.e. family, genus or species) in my study. A fine scale (stand level) radio tracking study in France also found that dead trees are of greater importance to roosting ecology than other woodland characteristics such as tree height (Rueegger et al., 2018). The biological relevance of increasing the amount of standing dead trees will vary depending on species. *B. barbastellus* activity is predicted to increase over 50% when additional standing dead trees are provided whereas *N. nyctalus* activity will increase at a lower rate.

Species richness, overall bat activity and many bat species were positively influenced by increasing light and no species or guild was negatively influenced. This can be interpreted in two ways; firstly that light penetrating the upper canopy will influence the temperature of tree roosts below, and secondly increasing light below the canopy is directly related to the openness of the canopy (i.e. as the canopy opens the light level increases). Although *B. barbastellus* regulates roost temperature through socio-thermoregulatory behaviour (Russo et al., 2017a), bats in general are thought to select day roosts based, in part, on their thermal properties (see chapter 3) and consequently the amount of light within a woodland interior will influence roost use and activity (i.e. bats moving to and from roosts and engaging in social behaviour around a roost). Although an increase in light levels was predicted to improve a woodland for *B. barbastellus* the relatively small increase in observed activity at sites with greater light levels (more open canopy) the biological relevance of this woodland characteristic is not as clear as increasing the amount of available tree cavities and standing dead trees.

Other woodland characteristics were found to be statistically significant but had a low effect size and so little biological significance.

2.5 Management recommendations

I found that UK forestry practices influence the richness and activity of bats and their insect prey. By exploring the effects of woodland characteristics on bat activity at different scales (i.e. combined, guild and species activity) commonalities are evident but importantly even species known to exploit very similar niches vary in their responses to management.

The sampled woodland thinning increased bat richness, probably because less below-canopy vegetation clutter provided opportunities for open and edge foraging species in addition to interior foraging species. Abandoned, and minimal intervention managed woodland were preferred by

tree-dwelling bats, probably as they provided more roosting opportunities than did intermediate and heavily thinned woodland.

All bats responded well to woodland characteristics that form in later successional stage woodlands. Managed woodland would be improved for bats by encouraging the characteristics one would expect in older woodland such as:

- Numerous standing dead and veteran trees.
- Tree cavities on all trees as a result of age or damage (e.g. frost cracks).
- An open canopy as a result of gap dynamics (i.e. ageing, damaged, dead and fallen trees).
- A heterogeneous canopy architecture.
- A reduction in below-canopy vegetation clutter

In contrast, insect numbers peaked in early stage successional woodland with dense below-canopy vegetation clutter. A mosaic of woodland characteristics including dense and sparse understory clutter would provide habitat suitability for bats and their prey.

The UKWAS certification recommends $20m^3$/ha of standing and fallen deadwood should be achieved to promote biodiversity in sustainably managed woodland (UKWAS, 2017). I found that the number of standing dead trees was more than triple, and the number of tree cavities was more than five times higher in unmanaged woodland than their paired sustainably managed equivalent. The sustainable certification standard should (1) separate the requirements for the amounts of fallen and standing dead trees, (2) triple the recommended requirement for the volume of deadwood and (3) include a new recommendation that promotes cavities in all trees (not just standing dead trees). The advice that woodlands should be managed to encourage the restructuring of even-age stands appears to be creating managed woodlands that are of similar stand structure to under-managed and abandoned woodland, which is encouraging for biodiversity in woodlands and should continue.

This chapter considers the effect of woodland management on bats and their insect prey and although commonalities to responses are evident, species-specific research that investigates the ecological requirements of woodland-dwelling bats is required. I now pursue this objective in chapter 3 by determining the importance of woodland that has sufficient and diverse tree roosting opportunities for the woodland specialist *B. barbastellus,* studied by radio tracking bats to roosts.

2.6 Supplementary material

During the first year of my PhD research I undertook a pilot study to test the efficacy of woodland survey methods and establish how many paired sites were needed to be confident of finding an effect of management on bat richness and activity, and how many nights of acoustic recordings were needed before bat richness plateaued (Fig. S2.7). Based on these results I selected to place acoustic detectors in each woodland for five nights and aimed to survey 29 sites.

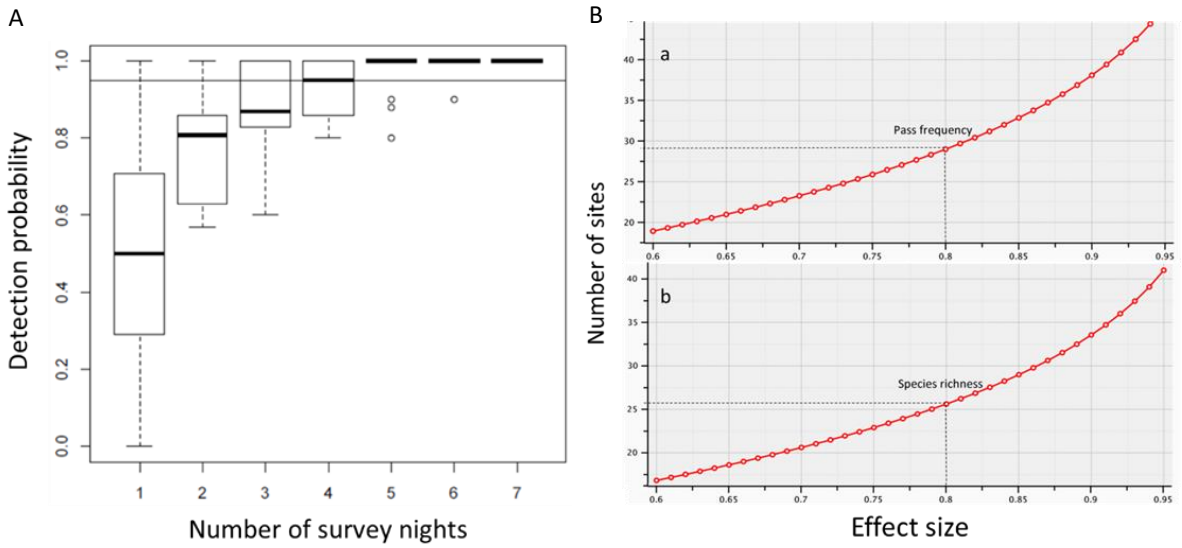


Figure S2.7 (A) Detectability curve for all species confirmed present by survey night seven determined by acoustic recording. The probability of detecting woodland bat species during an acoustic woodland survey at least once during *n* surveys is shown. Fourteen replicates were conducted (7 sites x 2 stands in each site). Horizontal line indicates 95% certainty. Probability is taken from species richness on cumulative survey days and set against species richness at night seven to find *p* for each survey night. Median 95% probability is reached at survey night four and the spread of data reduces at night five. The spread of data reduces over survey days increasing the confidence of reducing survey days without losing the detection of bat species echolocations. Based on these results I selected to place acoustic detectors in each woodland for five nights. (B) Power analysis using effect size (Cohen's d) formulated from the initial 2014 data (*n* = 7 sites). Cohen's d = mean difference/standard deviation. X-axis is the power and y-axis is the number of sites. To achieve power of 0.8 and be confident to identify an effect if present, 29 sites were needed for activity (pass frequency) and 25 sites for richness.

CHAPTER 3

Using ground-based and LiDAR-derived measurements to investigate scale-dependent selection of roost characteristics by the rare tree-dwelling bat, *Barbastella barbastellus*

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Abstract

Bats use roosts for protection, sociality and reproduction. Lack of knowledge regarding the specific roost preferences of tree-dwelling bats means that roosts are regularly removed from woodland during felling and thinning interventions, even when woodlands are managed to promote biodiversity. The often-unintentional loss of roosts this way continues to constrain efforts to conserve many rare bat species.

I investigated roost selection by *Barbastella barbastellus* in fragmented oak woodlands in southwest England. Twenty-nine bats were radio tracked to 44 tree roosts between 2007 and 2015. Twenty-four different characteristics of roosts were measured using a combination of ground-based field surveys and airborne light detection and ranging (LiDAR) imagery, and roost characteristics were compared with those of random trees to determine if roost selection occurred.

Bats selected trees in ancient semi-natural broadleaved woodland over other woodland habitat types. Standing dead oak (*Quercus* spp.), while scarce, was positively selected over other tree types and supported significantly more suitable roost cavities. Roost selection was most strongly influenced by the number of cavities present on a tree and the openness of the canopy around the tree. The height of roost cavities and distance to water were also important features that influenced selection. Pregnant and lactating bats switched roosts less frequently than post-lactating and nulliparous bats and selected cavities higher on trees, most likely to facilitate the development of offspring and reduce the risk of predation.

Old growth woodland is vitally important to *B. barbastellus* and so the preservation and restoration of these habitats should be a conservation priority. While standing dead trees supported more preferred roost cavities than other tree types, my findings indicate that any tree supporting a suitable cavity may be used as a roost, irrespective of the size, condition or species, and should be retained wherever possible. Promoting the natural succession of younger woodland will help to deliver additional sustained benefits in the future. Open source LiDAR imagery proved successful in

identifying woodland characteristics important to roosting bats and its future application has the potential to improve woodland structure measurements and reduce labour-intensive field surveying.

3.1 Introduction

The availability of suitable roosts influences the distribution, diversity, social structure and reproductive fitness of bats (Kunz and Lumsden, 2003). Roosts provide protection from predation and shelter from ambient environmental conditions and are important sites for mating, hibernation and rearing young (Kunz and Lumsden, 2003; Lacki et al., 2007; Willis and Brigham, 2007). When woodlands are subject to human intervention i.e. to increase economic yield, promote recreational use or to improve ecological function after degradation has taken place, these interventions can affect the availability and suitability of roosts. By identifying characteristics of tree roosts that are most important to bats a more directed and effective approach to woodland management can be undertaken that delivers improved conservation outcomes.

Meta-analyses have identified a number of habitat features that are typically important to tree-dwelling bats, including tree height and diameter, canopy closure, tree trunk girth and the occurrence of standing deadwood (Lacki and Baker, 2003; Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015a; Naďo and Kaňuch, 2015). The frequency, type and size of cavities have also been shown to influence roost selection (Russo et al., 2004; Lučan et al., 2009). In addition, bat presence within woodlands has been linked to the ruggedness (Froidevaux et al., 2016) and openness (Russo et al., 2004; Cox et al., 2016; Kortmann et al., 2017) of the upper canopy. Characteristics of the surrounding landscape do influence the value of woodlands to bats and their insect prey (Fuentes-Montemayor et al., 2013; Lintott et al., 2014c, 2015a). Favourable microclimatic conditions may increase roost suitability (Boyles, 2007) and the phenomenon of social thermoregulation driven by roost characteristics indicates that bats do not rely passively on ambient temperature while roosting (Willis and Brigham, 2007; Russo et al., 2017a). In certain landscapes, topographical characteristics such as elevation, terrain aspect and distance to water have also been shown to be important for determining roost selection (Cryan et al., 2000; Lacki and Schwierjohann, 2001; Lacki and Baker, 2003).

The importance of woodland characteristics can vary according to the sex and reproductive state of bats (Lintott et al., 2014). Breeding female *Plecotus macrobullaris*, for example, predominantly roost in tree cavities at lower elevations than non-breeding females, while males select roosts in rock cavities and man-made structures (Alberdi et al., 2015). Understanding variability in roost selection by other species during different reproductive stages requires further work (Jachowski et al., 2016).

Many tree-dwelling bat species form fission-fusion societies, whereby individuals roost with one another interchangeably (Fleischmann and Kerth, 2014), and regular roost switching by bats in these societies is well documented (O'Donnell and Sedgeley, 1999; Russo et al., 2005; Trousdale et al., 2008; Ngamprasertwong et al., 2014). The primary function of roost switching remains unclear although reducing parasite load and risk of predation, minimising roost fouling, maintaining social cohesion among individuals, and maintaining knowledge of the locations of available roosts have all been proposed as drivers (Owen et al., 2001; Russo et al., 2005; Kühnert et al., 2016). Maintaining knowledge of existing roosts may be particularly important due to the ephemerality of tree roosts (Trousdale et al., 2008; Russo et al., 2005) and the temporal variation in the thermoregulatory requirements of bats (Russo et al., 2017a). While frequent roost switching is commonly exhibited by some species, these species typically express high inter-annual fidelity to roosting sites, returning to the same breeding site each year (Hillen et al., 2010; Silvis et al., 2014).

Barbastella barbastellus (Schreber, 1774) is classified as 'Near Threatened' by the International Union for the Conservation of Nature (Piraccini, 2016), is listed under Annex II and IV of the EU Habitats Directive and is a UK Biodiversity Action Plan priority species (JNCC, 2010a). Throughout Europe, *B. barbastellus* has retained a strong preference for roosting in trees and require old growth broadleaved forests that provide a high number of suitable roost cavities (Russo et al., 2004, 2010). Historic declines in populations have been associated with loss of old growth broadleaved woodland habitat (Russo et al., 2004; Piraccini, 2016). To date, few studies have characterised the roosting requirements of *B. barbastellus*. Russo et al. (2004, 2010) and Kortmann et al. (2017) documented

roost preferences in breeding populations inhabiting extensive beech (*Fagus sylvatica*) and mixed upland forests respectively. Only limited data are available for the species within fragmented broadleaved woodlands at lower elevations that are more typical across the species' Europe-wide range. In the UK, ancient semi-natural woodland can be classified as fragmented stands of woodland, usually old growth, that have been wooded since before 1600 AD, and may or may not have been felled at some time in their history. Such fragments are the only representatives of truly natural woodland in the UK (FC, 2017).

There has been an increase in the use of airborne LiDAR (light detection and ranging) remote mapping technology for applications in forestry management (Lefsky et al., 2002), and more recently to study the interactions between woodland structure and woodland-dwelling animals (Müller et al., 2014; Hill and Hinsley, 2015). Measuring three-dimensional vegetation structure (Davies and Asner, 2014), upper canopy heterogeneity (Jung et al., 2012) or canopy architecture at the stand or woodland scale is either impossible to achieve using traditional survey methods (Davies and Asner, 2014), or requires a substantial amount of surveyor effort and money (Müller and Brandl, 2009). LiDAR technology also allows fine detail surveying of outer canopy architecture providing complex metrics of woodland structure (Vazirabad and Karslioglu, 2010).

I investigated the roosting requirements of female *B. barbastellus* in small fragmented broadleaved woodlands in southwest England using radio tracking to locate roosts and examine roosting behaviour. I recorded roost characteristics using a combination of terrestrial field surveys and airborne light detection and ranging (LiDAR) imagery and examined roost selection between early spring and late autumn at three spatial scales: (i) woodland structure and management type, (ii) tree type, and (iii) cavity type. I tested the hypotheses that bats selected roost characteristics at random on all levels by comparing the characteristics of roost features used by bats with those available at random. In addition, I examined whether the selection of roost characteristics and the frequency of roost switching is influenced by the reproductive state of female bats.

3.2 Materials and Methods

3.2.1 Study area

Bats were captured and studied between May and September in 2007, 2008 and 2015 in four ancient semi-natural broadleaved woodlands in Dartmoor National Park (3°54’49” W, 50°35’15” N), southwest England (Fig. 3.1).

Figure 3.1 Woodland study sites (black polygons) from top to bottom: Houndtor Wood (3°44’50” W, 50°36’24” N) (71 ha), Yarner Wood (3°43’35” W, 50°35’41” N) (150 ha), White Wood (3°51’40” W, 50°31’56” N) (241 ha), and Dendles Wood (3°56’59” W, 50°26’13” N) (50 ha), in Dartmoor National Park (grey polygon). Inset: location and boundary of Dartmoor National Park within the UK. Adapted from Ordnance Survey open data base map.

Each woodland roosting site, hereafter referred to as a ‘home wood’, was delimited retrospectively using natural features, such as woodland edge and valley ridges, and a maximum distance of 250 m from a roost i.e. the maximum distance that I recorded from a roost to its nearest woodland edge.

Each of the four home wood areas share similar topographic features, including steep Dartmoor intrusion granite slopes and Crackington Formation mudstone valley bottoms covered predominantly with pedunculate oak (*Quercus robur*), sessile oak (*Q. petraea*) and hybrids of these (*Q.* x *rosacea*). Climatic conditions within the region are wet and mild with mean summer (May-September) precipitation between 260-460 mm and mean temperature between 12-15°C. Historic and current management has resulted in mosaic woodland habitats surrounded by upland heath and agricultural land. For the purpose of this study, habitat types were grouped as (i) ancient semi-natural broadleaved woodland comprising predominately oak wood but also including ash and wet woodland types, (ii) broadleaved plantation ancient woodland (PAWS) comprising predominantly beech (*Fagus sylvatica*) planted in the 1960s but with remnant oak standards, (iii) conifer PAWS restocked with Douglas fir (*Pseudotsuga menziesii*) in the 1960s, and (iv) woodland scrub with mixed restocked and regenerating broadleaved species (Fig. 3.2).

Figure 3.2 Visual example of habitat types including (a) ancient semi-natural broadleaved woodland, (b) broadleaved plantation ancient woodland (PAWS), (c) woodland scrub, and (d) conifer PAWS. See section 3.2.1 for further habitat descriptions.

3.2.2 Bat capture, marking, tracking and monitoring

Barbastelles were captured by using 2.6 and 6m length 38mm mesh 4 shelved bat mist nets (Avinet Inc., Portland, US) and 2 bank harp traps (Faunatech Austbat, Victoria, Australia) placed along woodland rides, and at roost trees during emergence with large hand nets (net diameter 47 cm, net depth 78 cm) attached to extendable aluminium poles. Apodemus acoustic lures (Apodemus field equipment, Mheer, Netherlands) and Sussex Autobat lures (University of Sussex, Sussex, UK) broadcasting direct recordings and synthesised *B. barbastellus* social and echolocation calls, respectively, were used to improve capture success (Hill and Greenaway, 2005; Scott and Altringham, 2014; Lintott et al., 2014b) in open woodland. Acoustic lures were not used at roost trees.

After recording biometric data, caught bats were fitted with lightweight radio transmitter tags (Pip3, 0.45 g; Biotack Ltd., Wareham, UK). Tags were glued between the scapulae using a biodegradable adhesive (Salts Healthcare Ltd., Birmingham, UK) after clipping the fur. All transmitters weighed < 5% of the body mass of the bat to avoid potential load-related changes in behaviour (Teague O'Mara et al., 2014). Bats were fitted with 2.9 mm aluminium wing bands (Porzana Ltd., Sussex, UK) to allow identification of recaptured individuals. All activities were conducted under Natural England licences 2015-8106-SCI-SCI-1 and 20082206.

Bats were tracked daily on foot to roost trees using r-1000 (Communications Specialists Inc., Orange, US), SRX 400 (Lotek Engineering Inc., Ontario, Canada) or Sika (Biotrack Ltd., Dorset, UK) radio receivers and three-element Yagi antennas (Wildlife Materials Inc., Murphysboro, US). Tree cavities were located using a directional antenna and binoculars from the ground, and later confirmed by undertaking dusk emergence surveys using Bat Box Duet bat detectors (Batbox Ltd., Sussex, UK), Song Meter 2 static detectors (Wildlife Acoustics Inc., Maynard, US) and a bespoke portable CCTV video system (Young et al., 2018).

3.2.3 Ground-based surveys of habitat characteristics

To investigate whether *B. barbastellus* selected roosts with particular characteristics, 16 habitat features that were considered to be biologically relevant for tree-roosting bats in the literature (Lacki and Baker, 2003; Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015a; Naďo and Kaňuch, 2015) were measured on the ground or in QGIS (Quantum Development Team, 2015; version 2.8.1 Wien) and compared with those recorded from randomly selected trees at the plot, tree and cavity scale. Random trees were selected by identifying the nearest potential roost tree to randomly selected point locations within home wood areas. Only trees that were equal to or larger than the smallest roost tree recorded in this study, determined by diameter at breast height (DBH), were selected as random trees. The number of random trees that I recorded data from was equal to the number of roost trees identified in this study (n = 44).

Characteristics measured in QGIS at the plot scale for roost and random trees included elevation, distance to water, distance to woodland edge, distance to public footpath and distance to potential sources of disturbance such as roads and buildings. Characteristics measured on the ground at the plot scale included terrain aspect, terrain slope and tree density. Tree density was measured using a point-centre quarter method (Causton, 1988; Russo et al., 2004), whereby the distance from each roost or random tree (point-centre) to its four nearest-neighbour trees (one in each quadrant around point-centres) was recorded and tree density calculated in hectares as 10000/(mean of the distances between point centres and the four nearest-neighbour trees)^2.

Characteristics recorded at the tree scale included tree type, height, DBH, number of cavities present, and percent canopy gaps assessed visually from the base of the tree. Tree types were categorised as follows: (i) 'Class 1 *Quercus*' live trees (*Q. robur or Q. petraea* or *Q. x rosacea*) showing less than 80% dead limbs and loss of foliage; (ii) 'Class 2 *Quercus*' dead trees (*Q. robur or Q. petraea* or *Q. x rosacea*) showing 80% or greater dead limbs and loss of foliage; (iii) 'other broadleaved

species' (all live individuals); and (iv) 'conifer spp.' (all live individuals). *Q. petraea* was the dominant oak species within home wood areas.

To investigate roost cavity selection, random cavities were located along transects within woodlands that intersected the areas in which most *B. barbastellus* roosts occurred. The identification of cavities as potential suitable roost features for bats was determined by eye using binoculars from the ground and based retrospectively on the structure of roost cavities used by radio tracked bats. To minimise limitations associated with ground-based detection of cavities, cavity surveys were undertaken in winter when leaves were absent. In situations where trees supported multiple cavities, one cavity was selected at random. Variables measured at the cavity scale included cavity type, height and aspect. Cavity types were defined as either (i) bark plates, (ii) splits (including frost cracks, hazard beams and tear-outs, as described by Andrews (2013)), or (iii) rot holes.

3.2.4 Light detection and ranging imagery

Three-dimensional LiDAR point cloud data (collected in April 2010) were obtained from the UK Environment Agency (open source data; http://environment.data.gov.uk/ds/survey/). Using QGIS, I created a canopy height model (CHM) at 1 m resolution from a digital surface model (DSM) and digital terrain model (DTM) (Fig. 3.3). Several structural variables were derived from the canopy height model including canopy gaps, mean canopy height, canopy ruggedness, and standard deviation of canopy height. As I was interested in assessing roost selection at both the tree and the plot scale I defined two buffers of 2 m and 16 m (0.1 ha) radius, respectively, around roost and random point-centres and recorded each variable at each of these scales. Due to patchiness in the coverage of open-source LiDAR data, comparisons could only be made between 29 roost and random plots, respectively. Following Fabianek et al. (2015b), canopy gaps were defined as being >2 m^2, with a tree height that was one-third the height of the surrounding mean canopy. Canopy ruggedness, as defined by Froidevaux et al. (2016), was calculated in QGIS using a terrain ruggedness

index (TRI) algorithm (Wilson et al., 2007). Standard deviation of canopy height was used as an additional measure of upper canopy surface variability (Froidevaux et al., 2016).

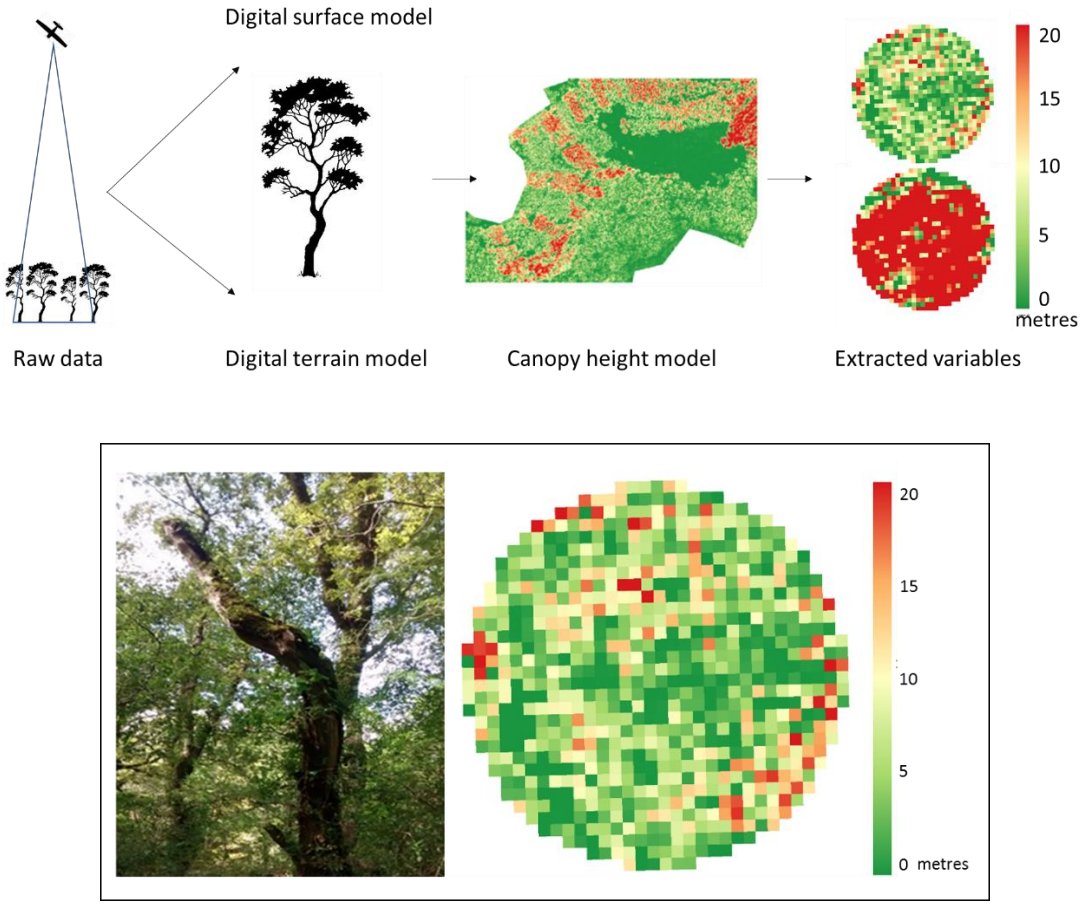

Figure 3.3 Airborne Light Detecting and Ranging (LiDAR) imagery workflow from flight pass data collection to extraction of variables using buffers of 2 m and 16 m radius around roost and random points. Inset: example of a canopy height model (right) for a 0.1 hectare area (16 m radius), surrounding a *B. barbastellus* roost within semi-natural broadleaved woodland (left), used to derive and compare mean canopy height and standard deviation, canopy gaps, and canopy ruggedness data. LiDAR resolution is 1 m^2. LiDAR images were created in QGIS (Quantum Development Team, 2015; version 2.8.1 Wien) using Environment Agency open source LiDAR survey data (http://environment.data.gov.uk/ds/survey/) and silhouette images replicated with permission from All-Free-Download.com.

3.2.5 Statistical analysis

3.2.5.1 Selection of woodland habitat type and tree type

To examine whether bats favoured roosts in a particular woodland habitat type or in a particular tree type, I used chi-square analyses to determine (i) whether use of a habitat type (number of roosts in each woodland habitat type divided by total number of roosts located in the study area) departed from that expected (area of corresponding woodland habitat type divided by the overall size of the study area), and (ii) whether the use of a tree type (number of roosts of each tree type divided by the total number of roosts in the study) departed from that expected (number of random trees of each tree type divided by the total number of random trees in the study). The Z statistic was used to calculate Bonferroni's confidence intervals (Neu et al., 1974) and to establish whether bats positively or negatively selected a woodland habitat type or tree type. For the analysis of habitat type selection, only data from Houndtor Wood were used as it was the only home wood area that contained all habitat types. To meet the assumptions of chi-square analysis, woodlands were grouped as 'ancient semi-natural broadleaved woodland' and 'other woodland' that included broadleaf PAWS, conifer PAWS and woodland scrub habitat types, and tree types were grouped as 'live *Quercus* spp.', 'dead *Quercus* spp.' and 'other tree types'.

3.2.5.2 Selection of roost features

To examine whether roost features differed significantly from random features, first I undertook a series of univariate analyses on the variables. T-tests were performed for parametric data while permutation tests (10,000 randomisations) were performed for non-parametric data. To determine which variables contributed most to explaining differences observed in roost and random features, I performed a series of generalized linear mixed models (GLMMs) using maximum likelihood estimations with binomial distribution and logit link function (lme4 package; R core team). I considered trees as my sampling units and included bat and site as random effects to control for variation among bats and sites (Bolker et al., 2008). Multicollinearity was assessed prior to model building using Spearman's correlation tests and using a $|r|>0.6$ coefficient threshold. When

correlation between variables was found, the variable with the least statistical explanatory power was removed to achieve model simplification. To provide meaningful comparisons of effect size, data were standardised using mean and standard deviation ($(x-\mu)/\sigma$). To identify the most parsimonious model that also explained the most amount of variance, Akaike's Information Criterion (AIC) adjusted for small sample sizes (AICc) was used. Pseudo R^2 (1-(residual deviance/null deviance)) was also applied for further consideration of model fit. A final set of models with only variables from the best fitting models using delta AICc (Δ_i) ≤ 2 was selected. For increasing precision in the calculation of estimates and associated standard errors, I applied a model averaging approach on the set of best models (Burnham and Anderson, 2002). Prediction curves were calculated for significant variables in the final model using GLMM estimates.

To examine whether the selection of roost features differed between bats of different reproductive states, bats were grouped as either (i) pregnant and lactating or (ii) post-lactating and nulliparous (i.e. bats showing no evidence of having bred), and differences between groups were compared using t-tests or permutation tests.

3.2.5.3 Roost switching behaviour

I calculated the frequency of roost switching in individual bats by dividing the number of times a bat switched roost by the number of days the bat was tracked. Bats were grouped as either (i) pregnant and lactating or (ii) post-lactating and nulliparous, and differences in the rate of switching between groups were compared using permutation tests.

All values of central tendency for normally distributed data are presented as mean ± standard deviation (SD), and for non-normally distributed data as median ± inter quartile range (IQR). When applicable data were tested for normality using Shapiro-Wilk tests. All statistical analyses were performed in R 3.1.3 and RStudio 1.0.143 (RStudio Team, 2015).

3.3 Results

In total 29 adult female *B. barbastellus* (see section 3.6 Supplementary material) were radio tracked to 44 roost trees between May and October 2007/2008 and May and October 2015. Bats were sampled by different surveyors (see Table S3.4 for details). Roost switching behaviour was determined for 27 bats, including pregnant (*n* = 4), lactating (*n* = 3), post lactating (*n* = 10) and nulliparous (*n* = 10) adult females. Bats were located within roost trees over consecutive days for between 3 and 18 days (mean 12 days ± 4.4 SD). Emergence counts (*n* = 59) revealed that roosts were occupied by 1–23 bats (mean 10 bats ± 6.5 SD; *n* = 36 roosts). Radio tracked bats expressed high fidelity to home wood areas and only rarely roosted in other woodland sites. Two individual bats caught in 2007 and 2008, respectively, were recaptured in the same home wood in 2015, providing evidence of inter-annual site fidelity to roosting sites.

3.3.1 Selection of woodland habitat type

Bats roosted in four woodland habitat types, including ancient semi-natural broadleaf woodland (*n* = 40 roosts), PAWS (broadleaf) (*n* = 1 roost), PAWS (conifer) (*n* = 2 roosts), and woodland scrub (*n* = 1 roost). Roosts within Houndtor Wood (*n* = 27) were not evenly distributed across habitat types ($\chi^2_{8.7}$, d.f. = 1, $p < 0.01$) with ancient semi-natural broadleaved woodland positively selected over all other woodland types (Fig. 3.4).

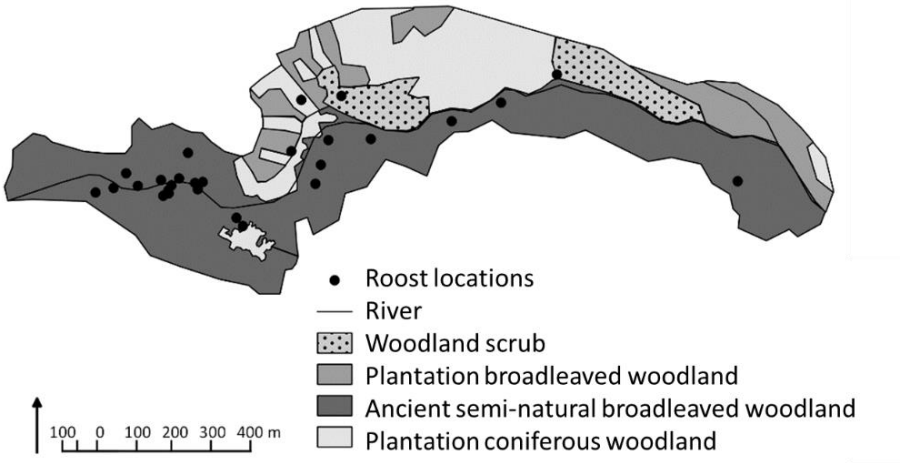

Figure 3.4 Home wood area within Houndtor Wood in Dartmoor National Park, showing the availability of four woodland habitat types (see section 3.2 for habitat type details) and the locations of 27 *B. barbastellus* tree roosts.

3.3.2 Selection of tree type

Roost trees consisted of live (*n* = 23) and dead (*n* = 20) *Quercus robur, Q. petraea* or *Q. x rosacea*, and one live *Fagus sylvatica*. Random trees consisted of live (*n* = 26) and dead (*n* = 4) *Q. robur, Q. petraea* or *Q. x rosacea*, 'other broadleaved' species (*n* = 9) and conifer species (*n* = 5). Tree type was not selected at random ($\chi^2_{76.4}$, d.f. = 2, $p < 0.001$) by bats. Dead *Quercus* trees were positively selected, live *Quercus* trees were used in line with availability, and all other tree types (*Fagus sylvatica*, *Betula pendula*, *Acer pseudoplatanus*, *Pseudotsuga menziesii* and *Pinus sylvestris*) were used less than expected. When I examined the number of cavities present on different tree types for the whole dataset that included all roost and random trees (*n* = 220 trees), I found significant differences ($\chi^2_{64.5}$, d.f. = 3, $p < 0.001$), with dead *Quercus* trees having significantly more cavities (median = 5.1, *n* = 42) compared to live *Quercus trees* (median = 1.1, *n* = 122), other broadleaved trees (median = 0.2, *n* = 33) and coniferous trees (median = 0.3, *n* = 23) (Dunn post hoc, $p < 0.001$), and live *Quercus* trees having significantly more cavities compared to other broadleaved (Dunn post hoc, $p < 0.01$) and coniferous trees (Dunn post hoc, $p = 0.02$) (Fig. 3.5).

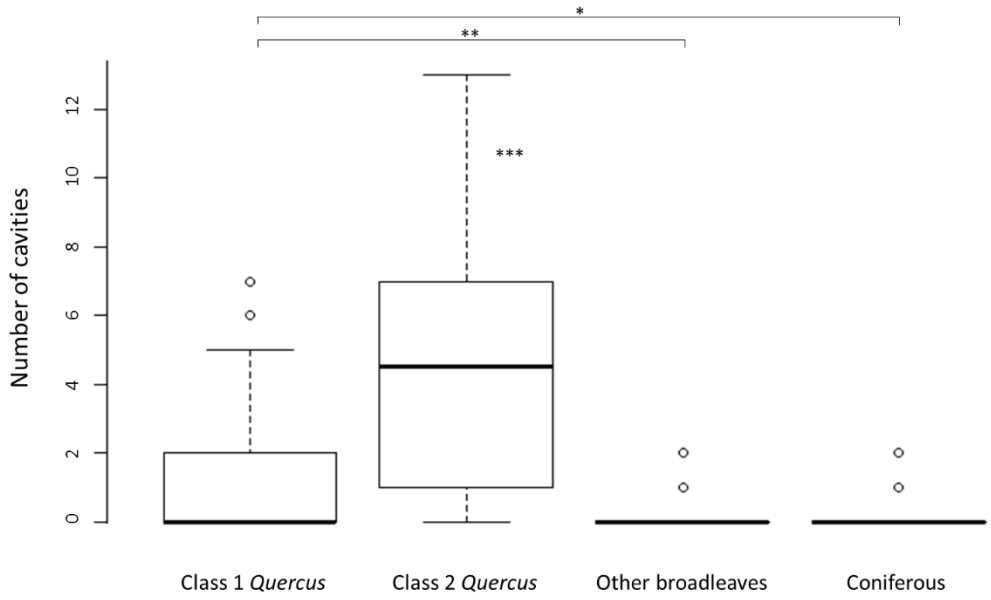

Figure 3.5 Median and inter quartile range for the number of cavities on roost and random trees (*n* = 220) according to tree type. Class 1 *Quercus* includes live oak trees showing < 80% of dead limbs and loss of foliage; Class 2 *Quercus* includes dead oak trees showing > 80% dead limbs and loss of foliage; other broadleaves includes *Fagus sylvatica* (European beech), *Betula pendula* (silver birch), and *Acer pseudoplatanus* (sycamore); Coniferous includes live *Pseudotsuga menziesii* (Douglas fir); and *Pinus sylvestris* (Scots pine). * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

3.3.3 Selection of roost features

Roost trees had a more open canopy structure at the tree (*n* = 44, perm, $p < 0.001$) and at 0.1 hectare around the tree (*n* = 29, perm, $p < 0.01$), were closer to water (*n* = 44, perm, $p < 0.01$) and had a greater number of cavities (*n* = 44 perm, $p < 0.001$) than random trees. No differences were found for each of the other variables that I examined (Table 3.1).

Table 3.1 Habitat variables recorded from roost and random plots (*n* = 44, or *n* = 29 for LiDAR datasets), roost and random trees (*n* = 44) and roost and random cavities (*n* = 41) used by adult female *B. barbastellus* (*n* = 29) radio tracked in Dartmoor National Park, Devon, UK. Values of central tendency for normally distributed variables (+) are presented as mean ± standard deviation, and for non-normally distributed variables (-) as median ± inter-quartile range. ns = not significant.

Scale	Habitat feature	Roost	*n*	Random	*n*	Source	*p* value	Distribution
Plot	Aspect	Categorical	44	Categorical	44	Field	ns	-
	Canopy gaps 2 m (%)	33 ± 29	29	33 ± 63	29	LiDAR	ns	-
	Canopy gaps 0.1 ha (%)	63 ± 14	29	41 ± 22	29	LiDAR	< 0.01	-
	Canopy ruggedness 2 m[†]	13820 ± 7561	29	12323 ± 7529	29	LiDAR	ns	+
	Canopy ruggedness 0.1 ha[†]	12871 ± 3799	29	12847 ± 5559	29	LiDAR	ns	+
	Distance to footpath (m)	87 ± 133	44	93 ± 93	44	QGIS	ns	-
	Distance to disturbance (m)	149 ± 169	44	140 ± 462	44	QGIS	ns	-
	Distance to water (m)	34 ± 32	44	72 ± 92	44	QGIS	< 0.01	-
	Distance to woodland edge (m)	52 ± 85	44	64 ± 84	44	QGIS	ns	-
	Elevation (m)	180 ± 39	44	193 ± 38	44	QGIS	ns	+
	Mean canopy height 2 m (m)	5 ± 4	29	7 ± 7	29	LiDAR	ns	-
	Mean canopy height 0.1 ha (m)	5 ± 3	29	7 ± 6	29	LiDAR	ns	-
	SD of canopy height 2 m (m)	4 ± 3	29	3 ± 3	29	LiDAR	ns	+
	SD of canopy height 0.1 ha (m)	5 ± 2	29	5 ± 2	29	LiDAR	ns	-
	Slope (%)	25 ± 25	44	25 ± 25	44	Field	ns	-
	Tree density (ha)[††]	145 ± 189	44	171 ± 293	44	Field	ns	-
Tree	Canopy gaps at tree (%)	63 ± 29	44	30 ± 15	44	Field	< 0.001	-
	DBH (cm)	57 ± 23	44	22 ± 6	44	Field	ns	+
	Number of cavities	4 ± 5	44	0 ± 0	44	Field	< 0.001	-
	Tree class	Categorical	44	Categorical	44	Field	< 0.001	-
	Tree height (m)	19 ± 7	44	22 ± 6	44	Field	ns	+
Cavity	Cavity aspect	Categorical	41	Categorical	90	Field	ns	-
	Cavity height (m)	7 ± 6	41	6 ± 9	90	Field	ns	-
	Cavity Type	Categorical	41	Categorical	90	Field	ns	-

[†]Canopy ruggedness score was calculated using terrain ruggedness index (TRI) (Wilson *et al*. 2007)

[††]Calculated in hectares as 10000/(mean of the four distances to nearest trees in metres)² (Russo *et al*. 2004).

Prior to fitting models, when I checked for correlations among variables I found that tree height, standard deviation of the canopy at 2 m and 0.1 ha, gaps at 2m and canopy ruggedness at 2 m and 0.1 ha were all correlated with one another, and tree type was correlated with canopy gaps and number of cavities. To avoid multicollinearity, tree height at 2 m, standard deviation at 2 m and 0.1

ha, and tree type were removed from models as they were found to be either not significantly different in univariate tests or were less significant than other correlated variables.

When I modelled variables at the plot scale, the model that best explained differences between roost and random trees included canopy gap at 2 m, canopy gap 0.1 ha, distance to water and elevation. At the tree scale, the best model included canopy gap at the tree, DBH, tree height and number of cavities on a tree, and at the cavity scale only cavity height was included (Table 3.2).

Table 3.2 List of habitat variables from the best generalized linear mixed effects models ($\Delta_i \leq 2$) at the plot, tree and cavity scale, including effect size, standard error, z statistic and *p* value. See Table 3.1 for units.

Model	Variable	Effect size	±SE	z	*p*
Plot	Canopy gap at 2 m	-0.5	0.4	-1.4	0.15
	Canopy gap at 0.1 ha	1.2	0.4	2.8	0.005
	Distance to water	-1.1	0.5	-2.5	0.01
	Elevation	-0.5	0.4	-1.4	0.15
Tree	Canopy gap at tree	1.2	0.4	2.8	0.007
	DBH	0.8	0.5	1.6	0.12
	Number of cavities	5.2	1.2	4.2	< 0.001
	Tree height	-0.2	0.4	-0.5	0.64
Cavity	Cavity height	-0.2	0.2	-0.9	0.33

DBH = diameter at breast height

When I fitted the nine key explanatory variables from the plot scale, tree scale and cavity scale models into a single model, three models performed equally well at explaining differences between roost and random trees, with each model containing one or more of the following variables: canopy gap at tree, canopy gap at 0.1 ha, cavity height, distance to water and number of cavities on the tree (Table 3.3). In the model that included all five variables, canopy gap at the tree and the number of cavities on the tree contributed significantly to explaining differences observed between roost and random trees, with number of cavities having the largest effect size (Fig. 3.6).

Table 3.3 Most parsimonious and best fitting generalized linear mixed effects models (Δ_i = ≤ 2) used to explain differences observed between roost and random trees. Shows the number of estimated parameters (K), differences between model second order Akaike's information criterion for small samples (AICc), the difference in AICc score (Δ_i) compared to the model with the lowest AICc score, Akaike weights (ω_i), and proportion of residual deviance explained by the model (Pseudo R^2). Final models have been averaged. See Table 3.1 for units.

Model	K	AICc	Δ_i	ω_i	Pseudo R^2
Canopy gap at tree + canopy gap at 0.1 ha + distance to water + no. of cavities	6	42.1	0.0	0.3	0.6
Canopy gap at tree + canopy gap at 0.1 ha + cavity height + distance to water + no. of cavities	7	42.5	0.4	0.2	0.7
Canopy gap at tree + distance to water + no. of cavities	5	42.8	0.7	0.2	0.6

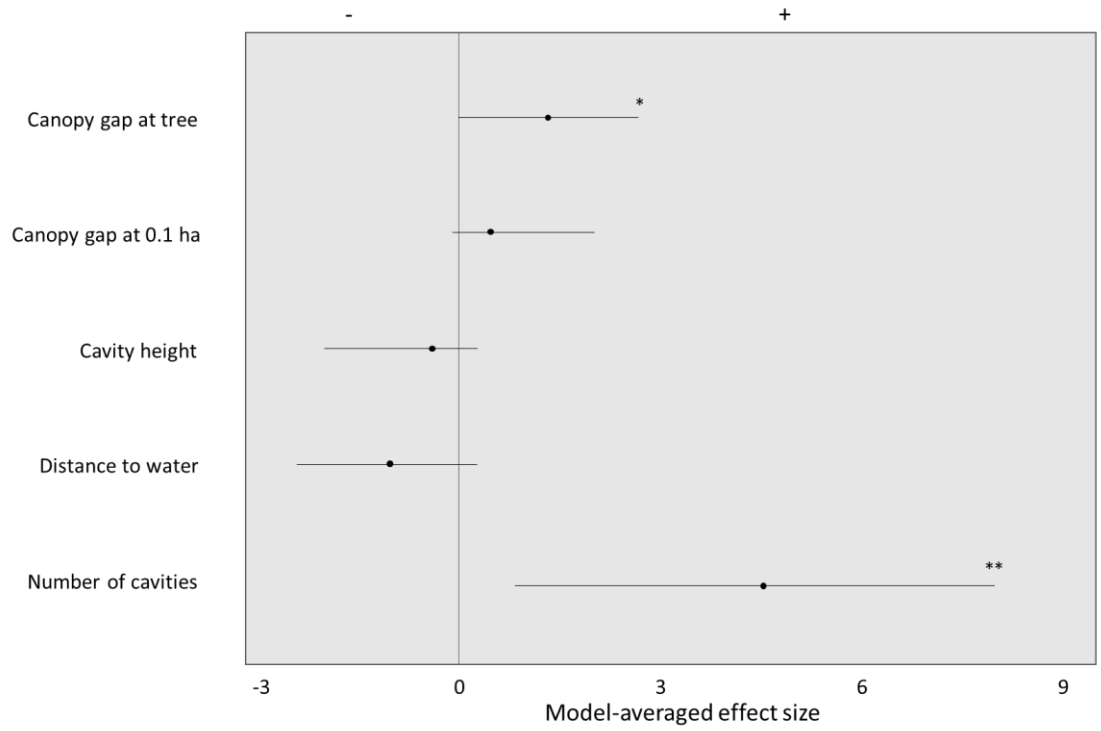

Figure 3.6 Variables included in the best generalized linear mixed effects models (Δ_i) showing model-averaged effect size (dot) and associated 95% confidence intervals (line) for each variable. Canopy gap at tree and number of cavities show a significant positive effect, and canopy gap at 0.1 hectare shows a non-significant positive trend on roost use. Cavity height and distance to water show a non-significant negative trend on roost use. * $p < 0.05$; ** $p < 0.01$. See Table 3.1 for units.

Predicted probability curves derived from the best generalized linear mixed model estimates for the two significant variables in the final model show probability of use by roosting bats positively increased with canopy gap around and number of cavities on a roost tree (Fig. 3.7).

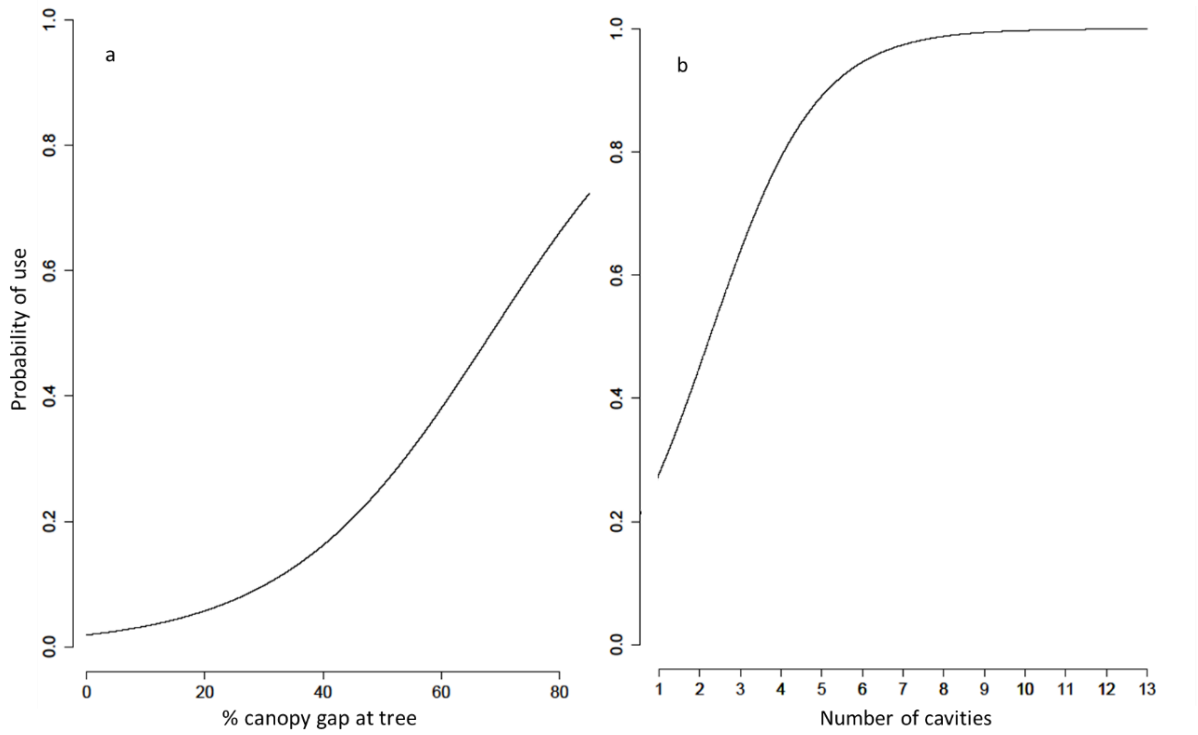

Figure 3.7 Estimated probability of use by *B. barbastellus* as a function of the significant variables (a) canopy gap at tree and (b) number of cavities on a tree. Prediction curves are derived from general linear mixed model estimates with the lowest second-order Akaike's information criterion for small samples (AICc).

3.3.4 Effects of reproductive state on selection of roost features

When I examined roost preferences according to the reproductive state of bats I found that pregnant and lactating bats used roost trees significantly further from water (n = 44, perm, p = 0.04) with fewer cavities (n = 44, perm, p = 0.03) and in cavities located higher on the tree (n = 41, perm, p < 0.001) compared to those used by post-lactating and nulliparous bats (Fig. 3.8). In addition, post-lactating and nulliparous bats roosted under defoliating bark more frequently (65% of roosts used)

than pregnant and lactating bats (44% of roosts used), although the difference between the two groups was not significant ($\chi^2_{11.3}$, d.f. = 2, p = 0.9). The majority of roosts used by pregnant and lactating bats were roosts of a more solid structure, such as splits and rot holes (56% of roost used). I found no difference for any of the other roost variables that I measured.

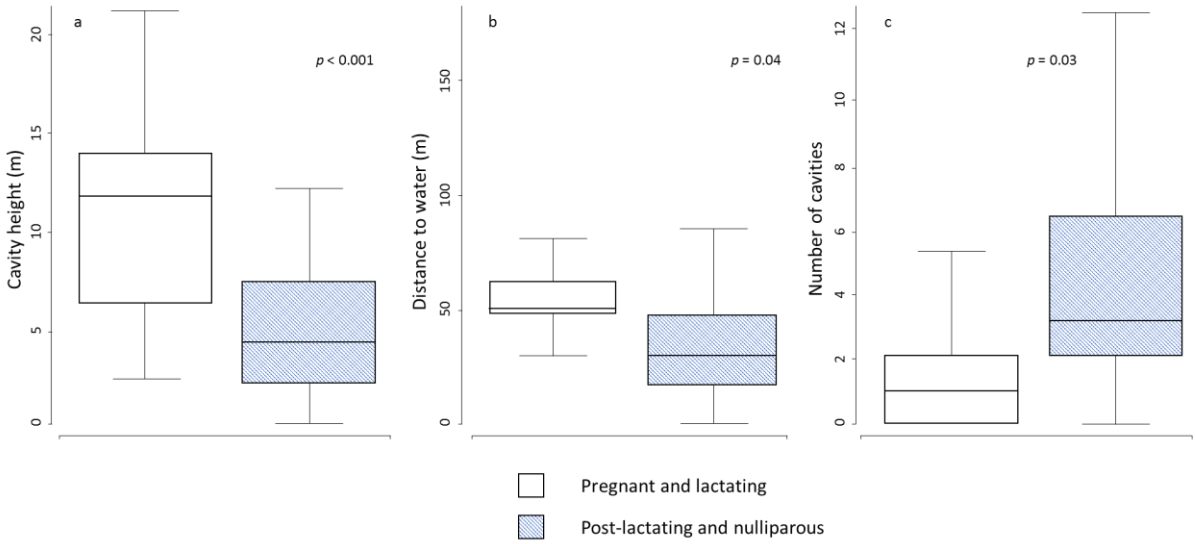

Figure 3.8 Median and inter quartile range for (a) cavity height (n = 41), (b) distance to water (n = 44), and (c) number of cavities (n = 44) as a function of the reproductive state of radio tracked adult female *B. barbastellus* (n = 29 bats).

3.3.5 Roost switching

Most bats (89%) switched roost at least once (median 0.4 ± 0.1 IQR switching frequency per day; range 0.3-0.6) during their respective tracked period, and occupied roosts for an average of 3.3 days (± 2.5 IQR; range 1-11 days) before moving. Pregnant and lactating bats (n = 7) switched roosts significantly less frequently (median 0.3 ± 0.1 IQR roost switches per day) than post-lactating and nulliparous bats (median 0.4 ± 0.1 IQR roost switches per day) (perm, p < 0.05).

3.4 Discussion

3.4.1 Selection of woodland habitat type

Selection of ancient semi-natural broadleaved woodland is common among insectivorous bats (Walsh and Harris, 1996; Russ and Montgomery, 2002; Russo et al., 2010), and roosting *B. barbastellus* significantly selected this habitat over other woodland types. Despite other studies finding a preference for roosting in beech forests (Russo et al., 2004), only one roost in this study was located in broadleaved plantation ancient woodland stands dominated by beech, despite its considerable availability within home wood areas, probably due to limited roosting opportunities as a result of the relatively young age of trees and ongoing harvesting within these stands. Indeed, Russo et al. (2010) recorded larger numbers of *B. barbastellus* roosts in unmanaged beech forests compared to stands that were periodically logged.

My findings, in agreement with those of Russo et al. (2004), demonstrate that minimal and non-intervention semi-natural woodland provide considerably higher roosting opportunities for *B. barbastellus* than other woodland types and so should be a focus for conservation efforts to protect the species. Initiatives to restore functioning old growth woodland such as the restoration of plantations on ancient woodland sites (Thompson et al., 2003) and rewilding (Monbiot, 2013) should be viewed as beneficial, and specific objectives to retain features associated with ancient woodland, in particular dead or decaying trees, should be a priority in all woodland types.

3.4.2 Selection of tree features

Bats selected roosts in trees that had a more open canopy structure than random trees, as has been observed elsewhere for *B. barbastellus* (Russo et al., 2004; Kortmann et al., 2017) and other echolocating tree-dwelling bats (Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015b). Much of this effect, however, may result from the strong selection by *B. barbastellus* of roost cavities in standing dead trees that had little or no canopy at all. Indeed, if accessibility is not hindered by branches, dense canopy may in fact be beneficial to *B. barbastellus* by facilitating earlier emergence times at

night and hence earlier foraging (Russo et al., 2007), and so the opportunity to select roost trees with specific canopy features may be limited by the availability of suitable roost cavities.

Roosts were more often located in oak trees (98%) than in other broadleaved or conifer species. Dead oak trees had significantly more cavities than other tree types. The value of standing dead trees as drivers of microhabitats such as roost crevices has been observed elsewhere (Paillet et al., 2017). The number of cavities on a tree had the largest effect on roost selection. This strong preference for roosting in dead oak trees has also been documented in Germany (Hillen et al., 2010), although roosts in other broadleaved tree types are not uncommon. Use of conifer species by *B. barbastellus* has been documented only rarely, such as in dead spruce trees killed by the spruce bark beetle *Ips typographus* (Kortmann et al., 2017). While the presence of a single suitable roost cavity on a tree may be sufficient, I propose that for *B. barbastellus* the overall value of a tree is likely to be positively correlated with the total number of cavities present because (i) more cavities on a tree increases the probability that at least one of them is suitable as a roost site at a particular moment in time, (ii) effort associated with searching for new roost options is reduced, and (iii) it is less risky to relocate to an alternative roost that is close during the day following stochastic events such as degradation of fragile bark plates in poor weather.

Pregnant and lactating female bats were located in trees with significantly fewer cavities compared to those used by post-lactating and nulliparous bats, probably because pregnant bats and bats with dependent young used solid cavity structures such as rot cavities and splits more frequently than post-lactating and nulliparous bats, which use bark plates more frequently (Russo et al., 2004). When bark plates develop on dead or decaying trees often many individual plates develop, providing numerous roosting opportunities for bats. Due to the low sample size (n = 9) for pregnant and lactating bats in this study, I recommend that further work be undertaken to identify with greater confidence the influence of reproductive state on roost selection in *B. barbastellus*.

3.4.3 Cavity selection

In this study, roost cavities were located lower on trees compared to random cavities. In contrast, in Italy Russo et al., (2004) described roost cavities that were higher on trees compared to randomly sampled cavities and suggested that bats may select higher cavities that benefit from higher roost temperatures as a result of increased exposure to solar radiation. While Russo et al. (2004) radio tracked mostly pregnant and lactating females, I studied mostly post-lactating and nulliparous bats. Indeed, when I compared groups in this study, I found that pregnant and lactating bats typically roosted in cavities that were higher on trees compared to post-lactating and nulliparous bats, supporting the hypothesis that females select higher cavities with greater exposure to solar radiation during pregnancy and lactation to benefit offspring development both *in utero* and *in situ* while in the roost (Russo et al., 2004). Indeed, at other times of year, when bats are neither pregnant nor have dependant young, it may be advantageous for females to roost in cavities that are cooler to facilitate torpor and conservation of energy (Willis and Brigham, 2007).

3.4.4 Distance to water

I found that roost trees were located significantly closer to water than random trees. The association with water has been shown elsewhere for *B. barbastellus* roosts using habitat suitability (Gottwald et al., 2017) and has also been observed in several other temperate forest-dwelling bats (Kalcounis-Ruppell et al., 2005; O'Keefe et al., 2009; Culina et al., 2017). Rivers that flowed through each study site were prominent features in the landscape and are probably used as flight corridors and drinking sites by bats. In contrast, *B. barbastellus* roosting in beech woodlands in Italy, which are regularly devoid of flowing water in summer, rely on cattle troughs as sources of drinking water (Russo et al., 2017b). Post-lactating and nulliparous bats were found in roosts significantly closer to water than pregnant and lactating bats, probably because pregnant bats and bats with dependant young primarily select roosts based on characteristics that benefit the development and safety of offspring rather than distance to water, which was easily accessible and not a limiting factor in each of the study areas. When water bodies are scarce in the landscape it is important to recognise that

urbanisation has shown to reduce the quality of these features to bats up to 3 km from the source of urbanisation (Lintott et al., 2015b).

3.4.5 Roost switching behaviour

As has been recorded elsewhere for *B. barbastellus* (Russo et al., 2004, 2005) and other tree-dwelling bats (Ngamprasertwong et al., 2014; Kühnert et al., 2016), I found that the frequency of roost switching during summer is lowest when bats are pregnant and lactating. Risk associated with moving non-volant dependant young between roosts is likely to be an important factor during lactation (Kühnert et al*.,* 2016) that overrides other potential advantageous associated with roost switching, such as minimising roost fouling or parasite loads within roosts. As bats are more sedentary during pregnancy and lactation, the use of more solid cavity structures is significant in that they provide greater protection against stochastic weather events that can remove ephemeral roost types such as bark plates and reduce risk of predation inside the roost itself. Indeed, I recorded a tawny owl *Strix aluco* on infrared video landing on the exit to a maternity roost inside a deep cavity in an oak tree when the colony was present there, presumably in an attempt to prey on the bats inside. Similar attempts at bark plates could easily result in the fragile plates becoming dislodged and exposing adult and young bats.

The overall rate of switching that I observed among bats radio tracked in this study highlights the large number of roosts that are likely to be required to support a colony of *B. barbastellus* within a woodland. I expect that at least 50 different roost cavities are used each year by the colony at Houndtor, which comprises between 20-30 adult female bats. A high annual turnover of new roost options is also likely to be important, as most roosts I found were under bark plates that may not remain intact over winter and be available for use again in the following summer.

3.4.6 The efficacy, application and limitations of LiDAR

Investigating habitat and roost use by bats in woodland has traditionally been explored through the use of terrestrial field measurements only (Lacki and Baker, 2003). Measuring three-dimensional

vegetation structure such as upper canopy heterogeneity (Jung et al., 2012) at the stand or woodland scale is, however, either impossible using traditional survey methods (Davies and Asner, 2014) or requires substantial resources (Müller and Brandl, 2009). Here, I show that LiDAR-derived measures of canopy structure provide an additional level of insight into roost selection that cannot be achieved easily through traditional survey methods. The use of bespoke airborne LiDAR datasets remains a barrier to some due to cost and lack of expertise needed to process raw data. However, it is notable that LiDAR surveying can be achieved at 5-10% of the cost of equivalent large-scale field surveying (Müller and Brandl, 2009) and in the UK processed open-source datasets have become more readily available in recent years. Several studies have derived informative variables from canopy height models that describe important habitat associations of animals (Hinsley et al., 2006; Müller and Brandl, 2009; Jung et al., 2012), and similar use of LiDAR datasets can be applied to bats to predict suitable roosting areas within woodland. While pairing temporally disparate LiDAR and wildlife survey datasets may present problems in some studies due to changes in habitat characteristics over time, effects of data lag in relatively slow changing habitats, such as woodland, is minimal over periods of up to six years (Vierling et al., 2014), which is longer than the time difference between LiDAR and *B. barbastellus* roosting datasets used in this study.

3.5 Management recommendations

Old growth woodland is vitally important to *B. barbastellus* and other tree-roosting bats and the preservation and restoration of these habitats should be a conservation priority. Intervention that removes maturing and standing dead trees is expected to significantly reduce the carrying capacity of a wood for cavity roosting bats and should be avoided wherever possible. In abandoned plantation broadleaved woodland, bats will benefit from non-intervention management to allow the natural maturation of the woodland and the gradual development of old growth characteristics, in particular standing dead trees and a more heterogeneous canopy structure. For plantation

woodlands in production, when thinning interventions are planned I advise the promotion of positive selection (i.e. removing trees that directly compete with neighbour trees that are marked to remain) over negative selection (i.e. removing all undesirable trees including badly shaped trees such as those that are forked, bent, heavily branched or damaged) (Kerr and Haufe, 2011) to ensure that as many roosting opportunities for bats are retained as possible. Standing dead trees do not compete for resources and should not affect the health or growth of the economic stock through direct competition, although I acknowledge standing dead trees can provide suitable habitat for tree pest species that could reduce the timber quality of neighbouring trees.

While standing dead trees typically provide more roosting opportunities for bats than other tree types, our findings demonstrate that roost selection by *B. barbastellus* bats occurs principally at the cavity level rather than on the characteristics of the tree, and so any tree supporting a suitable cavity may potentially be used by bats irrespective of the size, condition or species of the tree. As such, when undertaking thinning interventions within woodland it is important to identify the presence of potential roost cavities on all tree types prior to felling to ensure that as many of these features as possible can be retained. Indeed, I located roost cavities on young trees with small girths that would ordinarily be removed during thinning interventions. Tree age can be considered a unidirectional habitat filter (Pereira et al., 2004; Burgar et al., 2017) for tree-dwelling bats and so the value of young trees should be considered carefully in management plans to encourage the natural succession of veteran and standing dead trees and to provide sufficient turnover of suitable cavities over time. The use of artificial roosts such as bat boxes may be appropriate in young woodland to increase roosting opportunities for bats while waiting for the wood to mature naturally, although consideration should be given to the type of box and scale of use to ensure that rare species such as *B. barbastellus* are not unintentionally disadvantaged. Introducing chainsaw-carved cavities better mimics natural cavity thermal properties (Griffiths et al., 2018) and may be a better approach for increasing tree-roosting opportunity.

In Chapters 2 and 3 I presented results of research at the woodland scale. The importance of prey resources and the opportunities for foraging were further explored by radio tracking *B. barbastellus* to foraging grounds and identifying their prey using a molecular approach. These findings are presented in chapter 4.

3.6 Supplementary material

Table S3.4 Summary of all *B. barbastellus* (*n* = 29) captured and radio tracked to roosts 2007, 2008 and 2015. Season is determined using the meteorological calendar. Capture and radio tracking in 2008 and 2009 was undertaken by Matt Zeale; capture and radio tracking in 2015 were undertaken by myself.

No.	Date	Season	Age	Sex	Breeding status	Forearm (mm)	Body mass (g)	% tag weight
1	22/05/2015	Spring	Adult	Female	Pregnant	39.3	9.8	4.1
2	26/05/2015	Spring	Adult	Female	Pregnant	39.4	8.0	5.0
3	27/05/2015	Spring	Adult	Female	Pregnant	38.3	8.6	4.7
4	27/05/2015	Spring	Adult	Female	Pregnant	39.0	8.6	4.7
5	27/05/2015	Spring	Adult	Female	Pregnant	37.2	8.7	4.6
6	02/07/2015	Summer	Adult	Female	Pregnant	39.7	11.2	3.6
7	14/07/2015	Summer	Adult	Female	Lactating	39.4	10.0	4.0
8	30/07/2015	Summer	Adult	Female	Lactating	39.2	11.3	3.5
9	30/07/2015	Summer	Adult	Female	Lactating	39.8	9.6	4.2
10	13/09/2015	Autumn	Adult	Female	Non-breeding	39.8	10.0	4.0
11	13/07/2008	Summer	Adult	Female	Non-breeding	40.3	10.0	4.0
12	17/07/2008	Summer	Adult	Female	Post-lactating	39.2	9.1	4.4
13	31/07/2008	Summer	Adult	Female	Non-breeding	39.3	9.5	4.2
14	01/08/2008	Summer	Adult	Female	Non-breeding	37.7	9.1	4.4
15	01/08/2008	Summer	Adult	Female	Post-lactating	40.1	9.9	4.0
16	01/08/2008	Summer	Adult	Female	Non-breeding	40.0	9.1	4.4
17	01/08/2008	Summer	Adult	Female	Non-breeding	39.5	9.3	4.3
18	25/05/2007	Spring	Adult	Female	Non-breeding	38.6	8.9	4.5
19	08/06/2007	Summer	Adult	Female	Non-breeding	38.7	9.8	4.1
20	17/07/2007	Summer	Adult	Female	Post-lactating	39.9	9.1	4.4
21	23/08/2007	Summer	Adult	Female	Post-lactating	38.3	10.1	4.0
22	26/08/2007	Summer	Adult	Female	Post-lactating	39.9	9.0	4.4
23	26/08/2007	Summer	Adult	Female	Non-breeding	41.0	8.1	4.9
24	26/08/2007	Summer	Adult	Female	Post-lactating	38.9	9.3	4.3
25	26/08/2007	Summer	Adult	Female	Post-lactating	38.6	9.2	4.3
26	26/08/2007	Summer	Adult	Female	Post-lactating	39.2	8.6	4.7
27	26/08/2007	Summer	Adult	Female	Post-lactating	37.7	8.4	4.8
28	05/09/2007	Autumn	Adult	Female	Post-lactating	38.9	8.5	4.7
29	05/09/2007	Autumn	Adult	Female	Post-lactating	39.9	9.2	4.3

CHAPTER 4

The diet and foraging behaviour of a rare woodland-dwelling bat, *Barbastella barbastellus*: identifying habitat use and population trends of their insect prey

Abstract

The fragmentation and loss of foraging habitat, combined with reductions in insect prey are key factors for declines in bat populations. Identifying important bat foraging habitats and the conservation status of their consumed prey provides evidence for use in holistic management strategies for bat conservation.

I investigated home range use, habitat selection and foraging behaviour of *Barbastella barbastellus* at the northern edge of their global range by radio tracking bats (*n* = 7) to foraging sites and examining habitat selection using compositional analyses. I collected droppings from bats captured during flight (*n* = 28) at six sites and from a maternity colony. Prey DNA was extracted from 33 faecal samples using second generation high-throughput sequencing. Habitat compositional analysis and prey DNA sequencing data were combined to test the hypothesis that *B. barbastellus* feeds on insects with larval host food plants outside of the bats' foraging grounds. Finally I categorised consumed prey by their conservation status.

Individual *B. barbastellus* showed considerable variation in home range size (56.9-1293.3 ha) and nightly commuting distances (1.2-8.3 km), indicating that no obvious landscape barriers limit their movement. Foraging areas comprised only 5.8% (SD ± 3.7%) of home range area. All bats were faithful to their foraging grounds over the periods they were tracked. Lactating bats regularly returned at night to the woodland where their day roost was on the previous day, presumably to suckle their young. Riparian vegetation and broadleaved woodland were the foraging habitats most strongly selected. Hedgerows, within pastoral habitats, were also selected features within the landscape.

The number of prey species in individual faecal pellets (*n* = 28) was 5.9 (SD ± 3.2) and 10.6 (SD ± 4.9) in colony samples (*n* = 5). One hundred and nineteen prey species were confirmed from DNA barcodes, consisting mostly of moths (97.5%). Most prey species (97%) were categorised as having a larval stage dependent on host plants that are within the foraging habitats of *B. barbastellus*, or

were habitat generalists, rejecting the hypothesis that prey larvae require habitat outside of the foraging habitat of *B. barbastellus*. Interestingly, 67% of the caterpillars of consumed prey were associated with host plants located within hedgerows. Despite some consumed moths showing increasing population trends the overall finding is that *B. barbastellus* prey resource is reducing throughout southern England. This corresponds with *B. barbastellus* northern distribution and is a conservation concern.

Conservation management policies should target the protection and enhancement of key *B. barbastellus* foraging habitats within a 5.8 km radius of roost sites. Riparian habitat, broadleaved woodland and linear landscape features such as hedgerows should be managed to improve their value to foraging bats and all developmental stages of their prey.

4.1 Introduction

The loss and fragmentation of foraging habitat and reductions in insect prey have resulted in population declines of insectivorous bat species (Wickramasinghe et al., 2004; Rainho and Palmeirim, 2011; Muylaert et al., 2016). For a population of bats to survive and remain stable or to increase in numbers, productive foraging habitats are required. Foraging areas must (i) provide a suitable amount of prey, (ii) be structured to allow successful capture of those prey and (iii) be within an area that colony members can reach, both in terms of distance and the ability of the bats to traverse the landscape (Schnitzler et al., 2003). Radio telemetry studies are suitable for obtaining the spatial information required to assess home range areas (the total area used by an animal), sustenance zones (defined as the area surrounding a bat roost within which habitat availability and quality will have a significant influence on the resilience and conservation status of the colony using the roost (BCT, 2016)), and foraging areas (targeted areas of available habitat) (e.g. Entwistle et al., 1996; Bontadina et al., 2002; Zeale et al., 2012); and molecular dietary studies can highlight actions needed to protect prey resources (Arrizabalaga-Escudero et al., 2015).

DNA barcoding (Clare et al., 2009; Zeale et al., 2011) with high-throughput sequencing (Razgour et al., 2011; Hope et al., 2014; Salinas-Ramos et al., 2015) has been successfully used to identify consumed prey from bat faecal pellets with increased resolution than obtained by using traditional microscopic diet analysis. It is often possible to identify consumed prey in digested bat droppings to species resolution with high accuracy by using molecular methods (Zeale et al., 2011) providing conservation managers with evidence to protect those prey species and the habitats they require.

An animal with a specialised diet will be negatively impacted by a reduction in a single prey species. This is indeed the case for insectivorous bats that have reduced dietary breadths (Boyles and Storm, 2007). Investigating the conservation status and population trends of an animal's prey will identify current or perceived future prey impacts of changes in food resources. Furthermore, the prey of insectivorous bats may have more than one life stage (i.e. via metamorphosis) and their habitat

requirements may differ for each life stage. For example, the Mediterranean horseshoe bat (*Rhinolophus euryale*) consumes adult moths that often have larvae that feed in habitats outside of the bats' foraging habitats (Arrizabalaga-Escudero et al., 2015). This phenomenon is unlikely to be unique to this one bat species and emphasises the importance of research into life stages of prey items that are not necessarily eaten by bats, though which are vital for the viability and productivity of the prey species.

Barbastella barbastellus (Schreber, 1774) almost exclusively consumes adult moths captured on the wing (Zeale, 2011) and is considered to have a narrow dietary breadth relative to other insectivorous bats (Goerlitz et al., 2010). The bat is believed to target habitats associated with abundant moth prey, such as riparian habitats and broadleaved woodland (Greenaway, 2008; Zeale et al., 2012; Kokurewicz et al., 2017) and can travel large distances (20 km) to exploit these habitats (Zeale et al., 2012). Variation in selected foraging patches within and between seasons is apparent (Greenaway, 2008), possibly as a response to changes in prey availability. *B. barbastellus* is a suitable model species to investigate the foraging and dietary needs of woodland-dwelling insectivorous bats.

In this chapter I (i) describe the foraging and home ranges of *B. barbastellus* and investigate if the bats select specific foraging habitats within their home ranges, (ii) describe the diet of *B. barbastellus* using second generation high-throughput DNA sequencing, (iii) test the hypothesis that *B. barbastellus* prey require larval host food plants outside the bats' foraging grounds and (iv) investigate the population trends of moth species within the diet of *B. barbastellus*. *B. barbastellus* foraging behaviour has been explored in several studies (Greenaway, 2008; Hillen et al., 2009; Zeale et al., 2012; Kokurewicz et al., 2017), but to my knowledge this is the first-time that prey larval habitat requirements and conservation status has been considered within a foraging context.

4.2 Materials and Methods

4.2.1 Study area

B. barbastellus was studied at the northern edge of its global range (Piraccini, 2016) at seven sites in England (Fig. 4.1) including five broadleaved woodlands and one tithe barn (Table 4.1).

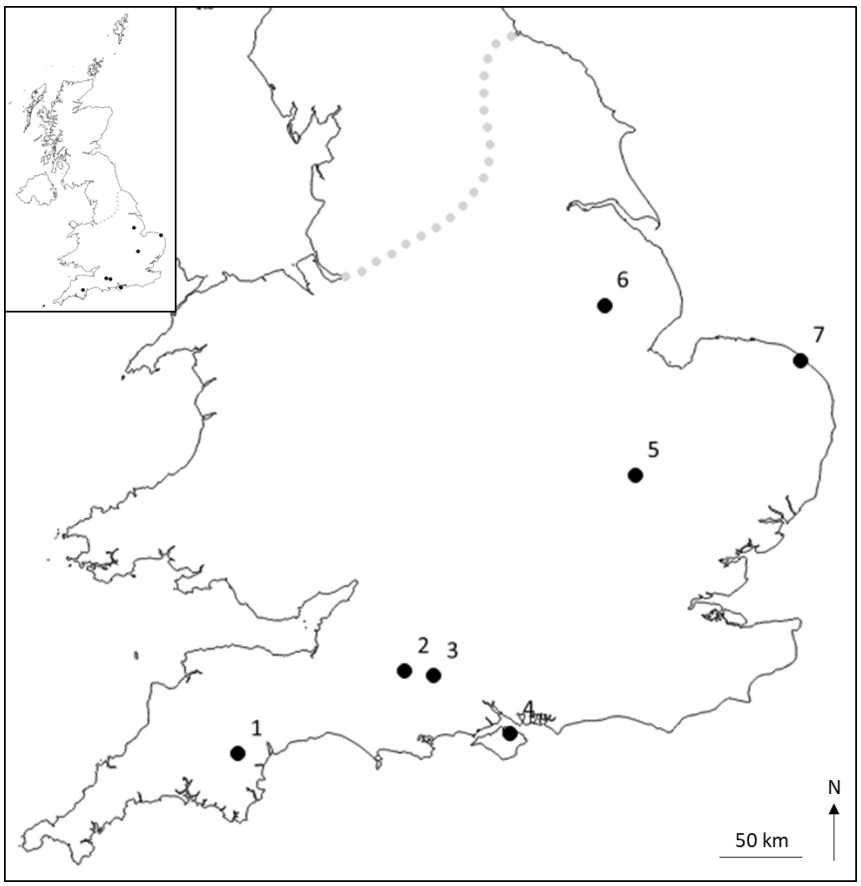

Figure 4.1 Study site locations (*n* = 7) used to capture bats and to collect faecal pellets. Free-flying *B. barbastellus* were captured and pellets collected from site 1 (3°43'35" W, 50°35'41" N), 2 (2°02'02"W, 51°04'49"N), 3 (0°22'54"W, 53°09'35"N), 4 (1°13'20"W, 50°42'42"N), 5 (2°05'21"W, 51°05'18"N) and 6 (0°01'56"W, 52°12'32"). Droppings were collected from beneath a maternity colony at site 7 (0°04'31"W, 51°59'34"N) and seven bats were radio tracked from site 1. The dashed grey line represents the likely northern boundary for the distribution of *B. barbastellus* within the UK when combining presence records (NBN gateway; https://nbn.org.uk/) and projected habitat suitability models (Zeale, 2011). Inset: map of Britain.

Table 4.1 List of key woodland characteristics of study sites 1 – 6 from which faecal pellets were taken from captured *B. barbastellus*. Woodland status = ASBW Ancient semi-natural broadleaved woodland, BW Broadleaved woodland, PAWS Plantation on ancient woodland site. See Handbook for Phase 1 Habitat Survey for category descriptions (JNCC, 2010b).

Site	Phase 1 habitat category	Woodland status	Main canopy species	Age (years)	Size (ha)	Aspect	Elevation (m)
1	A1.1.1	ASBW	*Quercus* spp.	>100	71	North	218
2	A1.1.2	BW	*Quercus* spp.	unknown	10	South	104
3	A1.1.1	ASBW	*Quercus* spp.	>100	75	North	21
4	A1.1.1	ASBW	*Quercus* spp.	>100	167	North	33
5	A1.1.1/A1.1.2	ASBW/PAWS	*Quercus* spp.	>100	16	North	124
6	A1.1.1/A1.1.2	ASBW/PAWS	*Quercus* spp.	>100	92	East	25

Bats were captured, and droppings collected, between April 2014 and September 2015 during their pregnancy, lactation and post-lactation periods. Bats were captured by mist nets, harp traps and acoustic lures following the procedures detailed in section 2.1.1). The ranging and foraging behaviour of *B. barbastellus* was sampled at site 1 between May and July 2015. Site 1 is a Special Area of Conservation (SAC), a semi-natural upland oak woodland in East Dartmoor Woods and Heaths National Nature Reserve (NNR) (3°43’35” W, 50°35’41” N). Sites 2-6 are all broadleaved woodlands, and all droppings were collected from bats captured in flight, within these woodlands. Site 7 is a well-established *B. barbastellus* maternity colony within a grade II listed medieval Tithe barn (0°04’31”W, 51°59’34”N) and is the only known example of a *B. barbastellus* colony in a structure built by people in the UK (Dunmore, 2002).

4.2.2 Bat capture, faecal pellet collection and tracking

To investigate ranging behaviour and to obtain faecal pellets for investigation of the diet of *B. barbastellus*, I captured bats at the same site described in chapter 3 (i.e. Site 1) using the same methods detailed in section 3.2.2. Faecal pellets from sites 2-6 were collected from captured free flying *B. barbastellus* by Ian Davidson-Watts. Capture, pellet collection and storage procedures were

identical to those used by myself. All samples were collected between May and September during 2014 and 2015. Bats were placed in sterilised hessian bags until they defecated (<30 minutes). The deposited faecal pellet was placed in a sterile collection tube, dampened with 96% ethanol, labelled and stored at -18°C. A single dropping was taken from each captured bat and analysed separately (section 4.2.5). I also obtained additional droppings collected from the ground below a maternity colony (site 7). These samples were collected monthly from April to August in 2015 and each sample consisted of *ca.* 10 pellets. To minimise the chance of these pellets being from other bat species any old pellets were swept from the floor before a white collection sheet was placed on the ground beneath the colony. Pellets were collected from the sheet within 24 hours of being deposited. Pellet collections were made by Jane Harris who has in-depth knowledge of this *B. barbastellus* maternity colony, and was confident that the droppings were from the target species by monitoring their location within the barn during each collection period.

The bats captured at site 1 were tracked using r-1000 telemetry receivers (Communications Specialists Inc, Orange, US) and three-element Yagi antennae (Wildlife Materials Inc, Murphysboro, US) continuously (Jones and Morton, 1992; Duvergé, 1996) using the homing-in method (White and Garrot, 1990). A bat was followed to foraging grounds by using a car. A tracking fix (surveyor location, distance (using signal gain), direction of signal and distance from signal) was taken every five to ten minutes throughout the night. Activity type was determined through the nature of the signal. A rapid directional signal was classified as coming from a commuting bat; a fluctuating signal within a defined area was classified as belonging to a foraging individual; a static signal was recorded as roosting behaviour (Russo et al., 2004; Zeale et al., 2012). Any night on which a signal was lost for a period of time resulting in less than 95% contact time was removed from analysis because the complete movements of the bat could not be described. Given the fast flight of the *B. barbastellus,* lost contact was a result of the bat moving rapidly from an area rather than because of equipment issues. In these instances the behaviour of the bat was unknown, and hence using this sub-set of data may have resulted in inaccurate conclusions or bias due to the species fast commute behaviour.

4.2.3 Habitat mapping

To inform habitat selection by foraging bats, I used habitat data taken from Zeale (2009) which was updated using GIS files (supplied by the Woodland Trust in 2015 and taken from Defra MAGIC map; http://www.natureonthemap.naturalengland.org.uk/; updated in 2014), aerial photographs dating between 2012 and 2016 (Google earth, version 6.2.2.6613) and through ground validation performed in 2016. Habitat maps were generated using Quantum GIS software (Quantum GIS Development Team 2015, version 2.8.1 Wien) using eleven dominant habitat types using Phase 1 habitat classifications (JNCC, 2010b) (Table 4.2).

Table 4.2 Description of habitat types used to assess habitat selection by foraging *B. barbastellus* with Phase 1 habitat classifications and codes (JNCC, 2010b).

Habitat type	Description
Broadleaved woodland	Semi-natural and plantation broadleaved woodland (A1.1). Dominated by trees more than 5 m high when mature with 10% or less conifer in the canopy.
Mixed woodland	Semi-natural and plantation woodland (A3). Dominated by trees more than 5 m high when mature with 10-90% of either broadleaved or conifer in the canopy.
Coniferous woodland	Semi-natural and plantation conifer woodland (A1.2). Dominated by trees more than 5 m high when mature with 10% or less broadleaved in the canopy.
Scrub	Dense and continuous or scattered woodland scrub (A2). Small shrubs and bracken patches were also included.
Unimproved grassland	May be rank and neglected, mown or grazed grassland on enclosed land. Not treated with application of artificial fertiliser or herbicide, or have been so intensively grazed or drained, as to alter the sward composition significantly, including all unimproved areas, neutral, acidic or calcareous (B1,2 and 3).
Improved grassland	Enclosed meadows and pastures which have been so affected by heavy grazing, drainage, or the application of herbicides and/or inorganic fertilisers that they have lost many species which one could expect to find in an unimproved sward (B4) Amenity grassland is also included (J1.2).

Arable	Ploughed land, cropland and recently reseeded grassland (J1.1). Includes arable land and grassland in rotation, horticultural land and nurseries, and recently planted and established orchards.
Riparian	Marginal vegetation around any water body (F2.1). Riparian woodland, swamp vegetation (F1) and all types of fen and mire (E).
Open water	Running and standing water (G). Includes rivers, streams, lakes, reservoirs, pools, flooded gravel pits, ponds, water-filled ditches, canals and brackish lagoons.
Urban	Any built up area (J3). Includes roads, houses and residential land, commercial retail, industry, high density residential (>40% cover), agricultural buildings, transport areas and restored or active landfill sites.
Upland moor	Unenclosed areas of unimproved upland heathland habitat (D), often grazed, including wet and dry shrub heath, heath grassland mosaic, gorse and bracken (C1).

Hedgerows (J2.1-4) and minor tree lines, where present as secondary habitats, were included in grassland, arable, riparian and urban categories.

4.2.4 Analysis of foraging grounds

To examine habitat preferences, first I took steps to improve the accuracy of radio tracking fixes recorded from tagged bats by placing a radio transmitter tag at a fixed position in the field and measured signal strength at varying distances and angles from the tag. This provided a reference for signal detection against which positional fixes of tagged bats could be calibrated. I then digitised radio tracking fixes using Quantum GIS software 2.8.1 and the distance/azimuth Python plug-in 0.9.1 (Paulo and Laplante, Technology One). Digitised fixes were analysed using Ranges 7 (Anatrack Ltd, Dorset, UK) to calculate maximum convex polygon (MCP) home range areas and cluster cores. Cluster analysis is considered the best approach for quantifying the core areas used by free-flying bats studied by radio tracking as it produces a representative depiction of foraging grounds (Zeale et al., 2016). I used MCPs to determine total area covered (foraging, roosting and commuting) by individual bats (using all fixes obtained from the bat concerned) and total colony area (all fixes from

all tracked bats) and established foraging areas using utilisation distribution discontinuities in intervals of 5% (Zeale et al., 2016).

I then examined habitat preferences by comparing the habitat composition in which each bat was recorded foraging (cluster cores) with the habitat available to them (individual MCPs). Compositional analysis was used to determine whether habitats were used in proportion to availability, or if selection was occurring, to determine the ranking of habitat types (Compositional Analysis Plus Microsoft Excel tool 6.2, Smith Ecology Ltd, Wales, UK) (Zeale et al., 2016). To satisfy the assumption that habitat categories should be one less than the number of tracked animals (Aebischer et al., 1993) the 11 habitat types were grouped into six broad habitat categories, i.e. arable (J1.1), moorland (D), pasture (B1-4 and J1.2), urban (J3), wetland (F1, F2.1 and E), and woodland (A1-3). These six broad habitat categories were classified as either foraging or non-foraging grounds based on habitat preference from compositional analysis.

4.2.5 Faecal DNA extraction, PCR amplification and sequencing

Prey DNA was extracted from faecal pellets using a QIAamp DNA Stool Mini Kit (Cat No./ID: 51504; Qiagen Ltd, UK) and amplified by Polymerase Chain Reactions (PCRs) at Queen Mary University London (QMUL) using a standardised top-down approach following the technique used by Salinas-Ramos et al. (2015). CO1 primers ZBJ-ArtF1c and ZBJ-ArtR2c (Zeale et al., 2011) were used for high-throughput next generation sequencing using adaptors for Ion Torrent (Piñol et al., 2014), as these primers have shown to be effective at amplifying arthropod prey while avoiding amplification of non-target DNA such as bat, bacteria and fungi (Zeale et al., 2011). The primers used may have low success with some taxa (e.g. Coleoptera) or may show taxon biases (Clarke et al., 2014), so absence in DNA records may not always mean absence in diet.

The obtained molecular sequences were then analysed using the Galaxy platform (Goecks et al., 2010). Reads were separated by forward and reverse MIDs (Multiplex Identifiers) with a maximum of two mismatches allowed (Salinas-Ramos et al., 2015). All sequences shorter than 147 base pairs or

longer than 167 base pairs (target amplicon length was 157 base pairs) were filtered out, collapsed into unique haplotypes before singleton sequences (a sequence occurring only once) were excluded from analysis.

4.2.6 Prey species identification and analysis of consumed prey

To investigate which prey species had been consumed by *B. barbastellus*, I ran the extracted DNA sequences through the Basic Local Alignment Search Tool (BLAST; http://blast.ncbi.nlm.nih.gov/Blast.cgi) and interpreted the results using taxonomic hierarchy with MEGAN6 software (Huson, 2016) using 281 BLAST score and a threshold of 98.5% sequence similarity for species identification based on mean sequence divergence values estimated by Zeale et al., (2011) for the amplified COI region. Even with this conservative approach some sequences were assigned to more than one species either within the same genera or family. To address this problem, I adopted a procedure used by Razgour et al. (2011) and Hope et al. (2014) which includes additional criteria to create identification confidence levels as follows:

1. Solid match (>98.5%) to one species - species-level assignment, or match (>98.5%) to more than one species, all belonging to the same genus - genus-level assignment.

2. Match (>98.5%) to more than one species belonging to different genera, only one of which was a UK species - species-level assignment to UK species.

3. Match (>98.5%) to several species of different genera within the same family or to reference sequences only identified to the family-level - family level assignment.

4.2.7 Prey larval habitat, conservation status and population trends

To establish the source habitat requirements of prey larvae, I searched for the host plants of the caterpillars of identified prey moth species in the Natural History Museum (London)'s database of the World's lepidopteran host plants (HOSTS) (Robinson et al., 2010), the UK Moths website (https://www.ukmoths.org.uk/) and reference books (Skinner, 2009; Waring and Townsend, 2009;

Sterling and Parsons, 2012). The larvae of moth species were then placed in categories adapted from Arrizabalaga-Escudero et al. (2015) as follows:

1. Foraging habitats: >60% of the larval host plants appear in *B. barbastellus* foraging habitat.

2. Non-foraging habitat: >60% of the larval host plants appear in *B. barbastellus* non-foraging habitat.

3. Generalists: where neither of the previous criteria is fulfilled, i.e. >60% threshold was not reached.

The conservation status of consumed prey was searched for in literature (Conrad et al., 2004; Fox et al., 2013). Where trend data were not available, that species was classified as 'data deficient' and not included in any category. Species were categorised as having a UK population trend that has (1) significantly declined, (2) significantly increased, or (3) been stable (i.e. no significant increase or decrease) between 1968 and 2007 (Fox et al., 2013). Only Macro-moths (typical wingspan >20 mm) were analysed as the data available for most micro-moths is limited.

All values of central tendency are means ± standard deviation unless otherwise stated.

4.3 Results

4.3.1 Bat capture and faecal pellet collection

Twenty-eight faecal pellets were collected directly from captured adult female (*n* = 20) and male (*n* = 8) *B. barbastellus* between April 2014 and September 2015 (including pregnant (*n* = 6), lactating (*n* = 6), post-lactating (*n* = 1) and non-breeding (*n* = 7) females). Droppings were collected from site 1 (*n* = 11), site 2 (*n* = 3), site 3 (*n* = 8), site 4 (*n* = 1), site 5 (*n* = 2), and site 6 (*n* = 3). DNA was extracted from a single pellet from each captured bat. Droppings were also collected each month between April and August 2015 (*n* = 5) from a maternity colony at site 7.

4.3.2 Ranging behaviour and foraging habitat selection

Seven female *B. barbastellus* (including pregnant (*n* = 3), lactating (*n* = 3) and nulliparous (*n* = 1) bats) from site 1 were radio tracked to foraging grounds for an average of 2.7 days (range = 2-3 days). The number of fixes per individual was 139 (SD ± 38). Bats showed considerable variation in MCP size (56.9-1293.3 ha) and maximum range (1.2-8.3 km) (Table 4.3). Weather conditions during tracking nights were mild and mostly dry. No extreme weather events occurred, and minimum night temperature remained above 5°C throughout the tracking period.

Table 4.3 List of radio tracked female *B. barbastellus* (*n* = 7) showing tracking start date, number of days tracked, reproductive status, maximum convex polygons (MCP), foraging cores, and mean maximum range travelled. Mean maximum range was calculated from the known roost used that day to the furthest point travelled that night. A bat was described as nulliparous ('unsure') when no signs of breeding were found.

Bat ID	Date tracked	# days tracked	Status	Foraging area (ha)		Mean max. range (km)	Foraging core % of MCP
				100% MCP	90% Core		
1	27/05/2015	2	pregnant	218.9	19.7	3.8	9.0
2	27/05/2015	2	unsure	477.6	14.7	5.2	3.1
3	27/05/2015	3	pregnant	56.9	5.7	1.1	10.0
4	02/07/2015	3	pregnant	575.7	27.9	7.7	4.8
5	14/07/2015	3	lactating	1293.3	22.6	8.3	1.7
6	30/07/2015	3	lactating	171.4	16.6	2.2	9.7
7	30/07/2015	3	lactating	462.5	10.2	5.4	2.2
Mean ± SD				465.2 ± 410.6	16.8 ± 7.5	4.8 ± 2.7	5.8 ± 3.7

Analysis of utilisation distribution discontinuities in intervals of 5% found that 10% of fixes from each bat disproportionately increased the range size (Fig. 4.2). Examination of these fixes identified that they were from bats categorised as commuting. Ninety percent cluster cores were therefore used to describe core foraging areas.

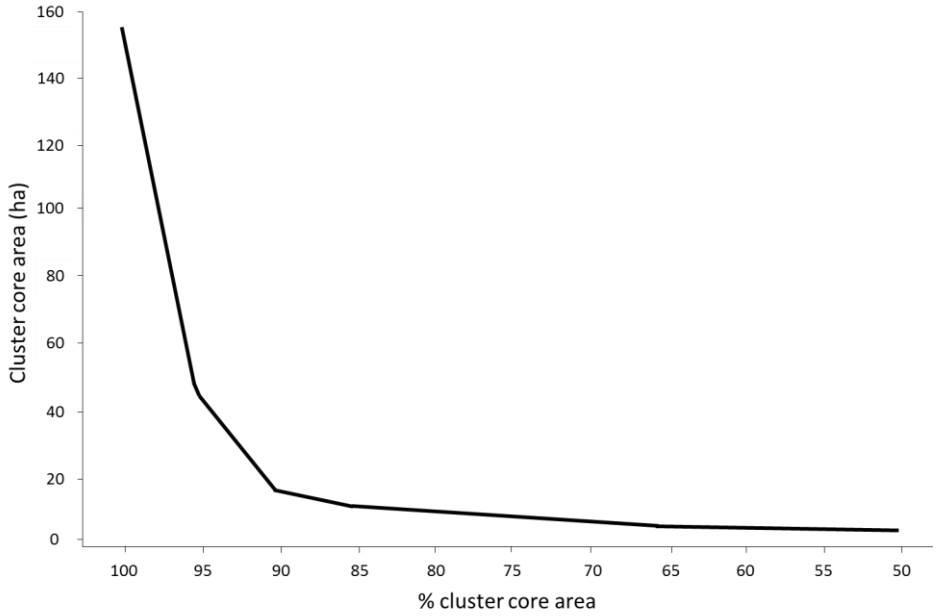

Figure 4.2 Utilisation distribution discontinuities in intervals of 5% for average cluster core areas for all tracked bats (*n* = 7). Ten percent of fix locations increased the size of foraging areas disproportionately. Examination of these fixes revealed that they were primarily recorded as bats commuted between roosts and foraging areas.

Core foraging areas were only 5.8% (± 3.7) of MCP areas (Fig. 4.3; Table 4.3). Foraging areas were away from the woodland in which the bat roosted (home wood) except for a pregnant bat, which foraged almost exclusively within the home wood (Fig. 4.4). Lactating females regularly returned to the home wood throughout the night (range = 2-3 times in a single night). Pregnant bats returned occasionally (range = 1-2 times in a single night) and not on every night that they were tracked. Bats showed high fidelity to presumed foraging sites over the period in which they were tracked ($\bar{x}$ = 6 days; range = 3-8 days), both for MCPs and 90% cluster cores.

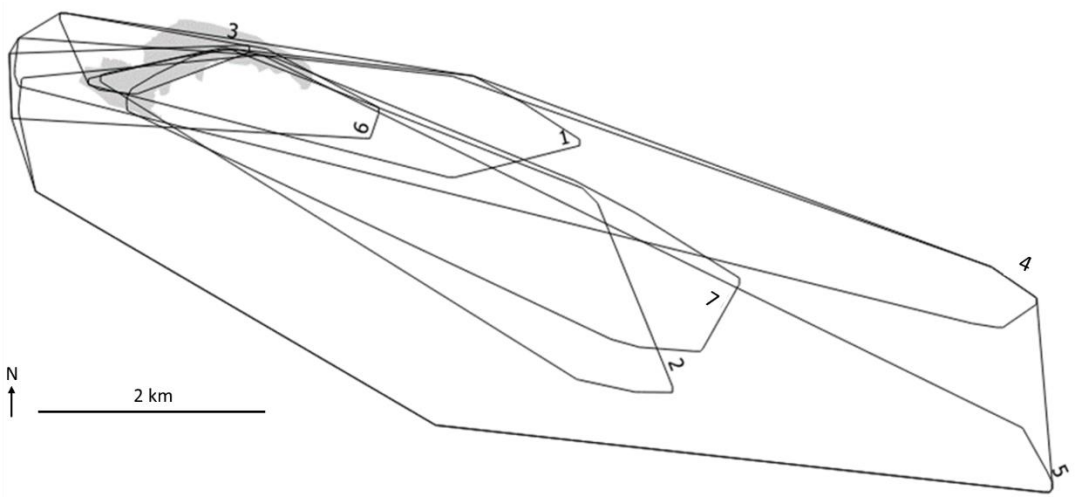

Figure 4.3 Individual maximum convex polygon (MCP) areas for each radio tracked *B. barbastellus* (numbered) and combined MCP for all seven bats (outer line). Numbers correspond to a bats ID (Table 4.3). The home wood (grey shaded polygon) is the woodland in which the bats roosted during the preceding day.

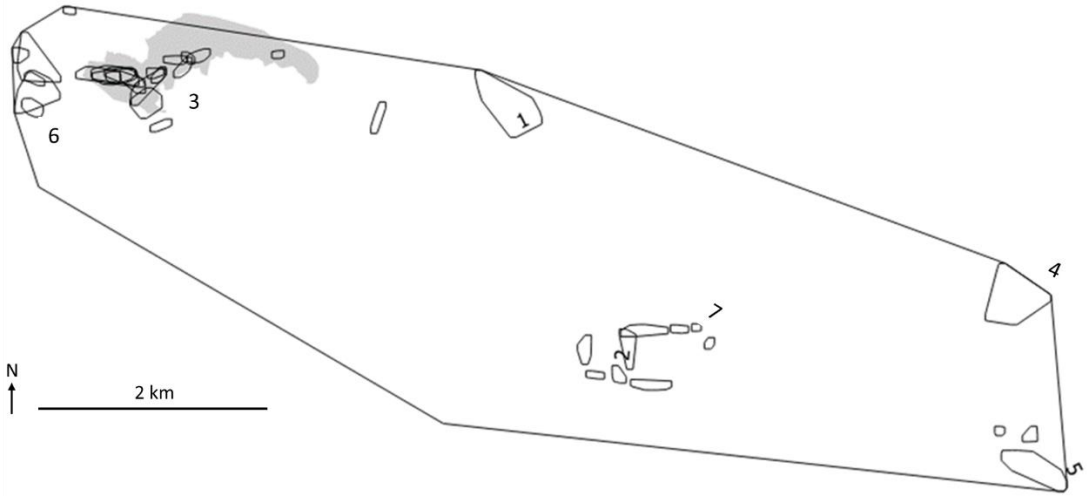

Figure 4.4 Individual core foraging areas defined as 90% cluster cores for each radio tracked *B. barbastellus* (numbered) and combined maximum convex polygon (MCP) for all seven bats (outer line). Numbers correspond to a bat's ID (Table 4.3). The home wood (grey shaded polygon) is the woodland each bat roosted during the day.

The proportion of habitats within the core foraging areas (90% cluster cores) of the radio tracked *B. barbastellus* (*n* = 7) was significantly different from the available habitat within their range (MCPs) (weighted mean Wilk's = 0.0123, χ^2_5 = 30.7747, $p < 0.01$). A ranking matrix (Table 4.4) shows the order of selected habitats as wetland > woodland > pasture > arable > urban >>> moorland (where > was preferred to that immediately following and where a >>> shows significant selection between the two adjacent habitat categories). The overall composition of available habitats (combined MCP = 1970.7 ha) shows that *B. barbastellus* were present in all habitat types but not evenly when comparable to habitat used most often (mean % habitat within 90% cluster cores; *n* = 7) (Fig. 4.5).

Table 4.4 Simplified ranking matrix for radio tracked *B. barbastellus* (*n* = 7) comparing proportions of habitat within used habitat (90% cluster cores) and available habitat (maximum convex polygons (MCPs)) showing preference for each category on every row compared to the corresponding habitat in each column. A significant difference between two habitats is shown as +++ (positive) and --- (negative), + or – shows a non-significant selection trend with rank order 5 being the most selected habitat type and 0 being the least selected.

	Arable	Moorland	Pasture	Urban	Wetland	Woodland	Rank
Arable		+	-	+	-	-	2
Moorland	-		---	---	---	---	0
Pasture	+	+++		+	---	-	3
Urban	-	+++	-		---	---	1
Wetland	+	+++	+++	+++		+	5
Woodland	+	+++	+	+++	-		4

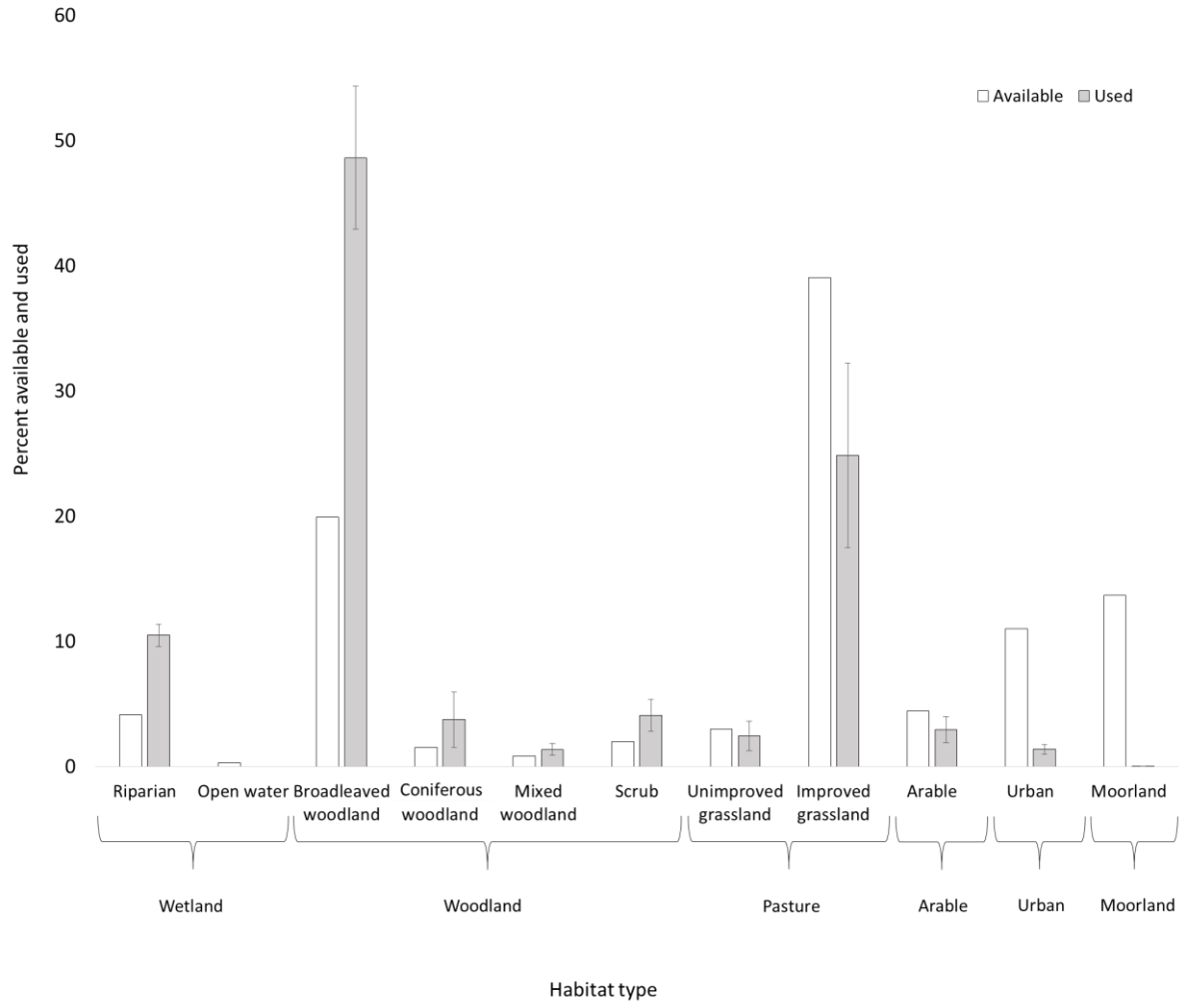

Figure 4.5 Comparison of the percentage of 11 available habitat types within the radio tracked *B. barbastellus* (*n* = 7) range (combined MCP) and core foraging areas (90% cluster cores) (mean % of area used) ± standard error in selection rank order of six broad habitat types (Table 4.4).

4.3.3 Diet composition

Prey DNA was successfully extracted from 33 faecal samples. Bioinformatics reprocessing and manual verification confirmed 205 prey DNA sequences belonging to the orders Diptera (*n* = 2), Lepidoptera (*n* = 202), and Neuroptera (*n* = 1). One hundred and twenty prey taxa were identified from 17 families (Table 4.5). The number of prey taxa per faecal pellet collected from captured bats (*n* = 28) was 5.9 (± 3.2) and from maternity colony samples (*n* = 5) was 10.6 (± 4.9). The number of prey taxa in colony samples varied by month; April (*n* = 8), May (*n* = 19), June (*n* = 11), July (*n* = 8),

August (*n* = 7). The majority of prey taxa appeared in only one or two faecal samples with the number of prey taxa appearing in three or more faecal samples (*n* = 21) included only 18% of the total confirmed prey items.

Table 4.5 List of prey (*n* = 120) identified in 33 *B. barbastellus* faecal samples using high-throughput molecular sequencing. Confidence levels follow Razgour et al. (2011) and Hope et al. (2014) based on the BOLD identification system, whereby confidence level 1 = solid match (>98.5%) to one species or match (>98.5%) to more than one species, all belonging to the same genus; level 2 = match (>98.5%) to more than one species belonging to different genera, only one of which was a UK species; and level 3 = match to several species of different genera, or to reference sequences only identified to family (>98.5%). Presence of ears (†) indicates prey items known to possess hearing-based defences against echolocating bats (Roeder, 1974; Scoble, 1992; Fullard, 1998).

Order	Family	Species	Confidence level	Sequence similarity	Number of pellets found within
Lepidoptera	Adelidae	*Nematopogon swammerdamellus*	1	100	1
	Coleophoridae	*Coleophora kuehnella*	1	99.6	1
	Crambidae†	*Eudonia lacustrata*	2	99	2
		Eudonia mercurella	1	99.6	2
		Eurrhypara hortulata	1	100	1
		Scoparia basistrigalis	1	99	3
		Udea lutealis	1	100	1
	Depressariidae	*Agonopterix heracliana*	1	99.6	1
		Carcina quercana	1	100	1
		Depressaria pastinacella	1	100	1
	Drepanidae†	*Polyploca ridens*	1	100	1
		Thyatira batis	1	100	1
	Erebidae	*Herminia grisealis*	1	99.6	2
		Herminia tarsipennalis	1	100	1
		Lymantria monacha	1	100	1
		Scoliopteryx libatrix	1	100	2
		Spilarctia luteum	1	100	1
	Geometridae†	*Aethalura punctulata*	1	100	1
		Alcis repandata	1	99.6	1
		Apocheima pilosaria	1	100	1
		Asthena albulata	1	100	2
		Biston betularia	2	99	1
		Cabera pusaria	1	100	2
		Cameraria ohridella	2	99.6	1
		Catarhoe rubidata	2	99	1

	Chloroclysta miata	2	99	1
	Chloroclystis v-ata	1	99.6	1
	Cosmorhoe ocellata	1	100	1
	Cyclophora annularia	1	99	1
	Dysstroma truncata	1	100	3
	Ectropis crepuscularia	1	100	1
	Electrophaes corylata	1	99.6	1
	Epirrhoe alternata	1	99.6	4
	Eulithis prunata	1	100	1
	Eupithecia abbreviata	1	99	6
	Eupithecia absinthiata	1	99.6	1
	Eupithecia exiguata	1	99.6	1
	Eupithecia plumbeolata	2	99	1
	Eupithecia subfuscata	1	100	1
	Eupithecia vulgata	1	99	1
	Gymnoscelis rufifasciata	1	100	2
	Hemithea aestivaria	1	100	1
	Hydriomena furcata	1	100	1
	Hydriomena impluviata	1	100	1
	Idaea aversata	1	99.6	2
	Idaea biselata	1	100	5
	Lampropteryx suffumata	1	99	1
	Lomaspilis marginata	1	100	2
	Lomographa bimaculata	1	100	1
	Odontopera bidentata	1	100	4
	Opisthograptis luteolata	1	100	2
	Peribatodes rhomboidaria	2	99	1
	Perizoma affinitatum	2	99	1
	Petrophora chlorosata	1	99	2
	Scopula floslactata	1	100	2
	Selenia dentaria	1	99	3
	Trichopteryx carpinata	1	100	1
	Xanthorhoe designata	1	99	1
	Xanthorhoe fluctuata	1	99	2
	Xanthorhoe montanata	1	100	5
Lymantriidae†	*Euproctis similis*	1	100	1
Noctuidae†	*Abrostola tripartita*	1	99.6	2
	Agrotis exclamationis	1	100	7
	Agrotis ipsilon	1	99	1
	Agrotis segetum	1	99.6	5
	Amphipyra pyramidea	1	100	3
	Anaplectoides prasina	1	99	1
	Apamea monoglypha	1	99	4
	Apamea sordens	1	99.6	1
	Atethmia centrago	1	100	1
	Autographa gamma	1	100	6
	Caradrina clavipalpis	1	100	1
	Caradrina kadenii	2	99.6	1
	Caradrina morpheus	1	100	1
	Cerastis leucographa	1	99.6	1
	Cerastis rubricosa	1	99	1
	Charanyca trigrammica	1	100	1
	Conistra vaccinii	1	99	1
	Cosmia trapezina	1	100	3

		Cryphia domestica	1	99.6	1
		Cucullia chamomillae	1	100	2
		Diarsia rubi	1	99	1
		Hoplodrina ambigua	1	100	3
		Hoplodrina blanda	1	99.6	1
		Hoplodrina octogenaria	1	100	1
		Hypena proboscidalis	1	100	1
		Lithophane socia	1	99	1
		Luperina testacea	1	99.6	1
		Mamestra brassicae	1	100	1
		Mesapamea secalis/didyma	3	99	2
		Mythimna impura	2	99.6	2
		Noctua comes	1	100	1
		Noctua fimbriata	1	100	1
		Noctua janthe	1	100	2
		Noctua pronuba	1	100	9
		Ochropleura plecta	1	99.6	3
		Oligia strigilis/versicolor	3	99.6	1
		Orthosia gothica	1	99.6	1
		Orthosia gracilis	1	99.6	1
		Orthosia incerta	2	99	2
		Phlogophora meticulosa	2	99	5
		Rivula sericealis	1	99.6	1
		Spaelotis ravida	1	99.6	1
		Xestia cnigrum	1	100	3
		Xestia xanthographa	1	100	3
	Nolidae	*Nola confusalis*	1	99.6	1
		Nycteola revayana	1	100	1
	Notodontidae†	*Notodonta ziczac*	1	99.6	1
		Pheosia gnoma	1	100	2
	Nymphalidae	*Maniola jurtina*	1	100	1
	Pyralidae†	*Cryptoblabes bistriga*	1	100	1
		Endotricha flammealis	1	100	3
	Tortricidae†	*Archips podana*	2	99.6	1
		Archips xylosteana	1	100	1
		Pammene fasciana	1	100	1
		Pandemis cerasana	1	99.6	1
		Pseudargyrotoza conwagana	1	99.6	1
Diptera	Drosophilidae	*Drosophila melanogaster*	1	100	1
	Scathophagidae	*Scathophaga stercoraria*	2	99	1
Neuroptera	Hemerobiidae	*Hemerobiidae* spp.	3	100	1

4.3.4 Prey larval habitat

One hundred of the 120 consumed prey taxa were successfully categorised as having their larval host plants in habitats associated with either (i) *B. barbastellus* foraging habitat, (ii) *B. barbastellus* non-foraging habitat or (iii) were considered generalists (see section 4.6 Supplementary material). The larvae of 19 species were not associated with a habitat due to having a food source other than

plants (e.g. fungi, mosses, insects, leaf-litter) as this study focussed on live plants to determine habitat requirement, and only species within the order Lepidoptera (all were moths) were included. Most prey species (79%) were categorised as having a larval stage dependent on host plants that were within *B. barbastellus* foraging habitats (wetland, woodland and pasture habitats). Only 3% of prey were found to feed on larval host plants located mainly outside *B. barbastellus* foraging grounds (arable, urban and moorland habitats). These included the flounced rustic (*Luperina testacea*) and large yellow underwing (*Noctua pronuba*) that feed on cultivated plants (although this species is known as commonly feeding on wild plants and grasses (Robinson et al., 2010)), and the brimstone (*Opisthograptis luteolata*) that specialises on plum trees (*Prunus* spp.). The remaining 18% of prey taxa larval host plants are located within *B. barbastellus* foraging and non-foraging habitats and so the larvae are considered generalists. Of the 100 categorised prey taxa, 67% of the caterpillars are associated with host plants located in hedgerows.

4.3.5 Prey conservation status and population trends

Of the total number of moths (*n* = 117) consumed by the sampled *B. barbastellus*, six were classified as Vulnerable by the IUCN red list of threatened species (http://www.iucnredlist.org/) including, *Atethmia centrago*, *Caradrina morpheus*, *Diarsia rubi*, *Hoplodrina blanda*, *Orthosia gracilis* and *Spilarctia luteum,* with each showing population reductions by more than 70% between 1968 and 2007 (Fox et al., 2013). In contrast, seven species including, *Abrostola tripartita*, *Chloroclystis v-ata*, *Lymantria monacha*, *Noctua pronuba*, *Noctua janthe*, *Nola confusalis* and *Trichopteryx carpinata* increased in abundance by more than 100% between the same period (Fox et al., 2013). Seventy-five moth species confirmed in the diet of sampled *B. barbastellus* have had their population trends monitored since 1968 (Fox et al., 2013). Of these 30.7% have significantly increased, 46.7% have significantly decreased, and 22.7% have stable populations. This is broadly similar to the known population trends of UK macro-moths, although double the number of species with increasing population trends were found in the diet of *B. barbastellus* compared with all species monitored (Fig. 4.6).

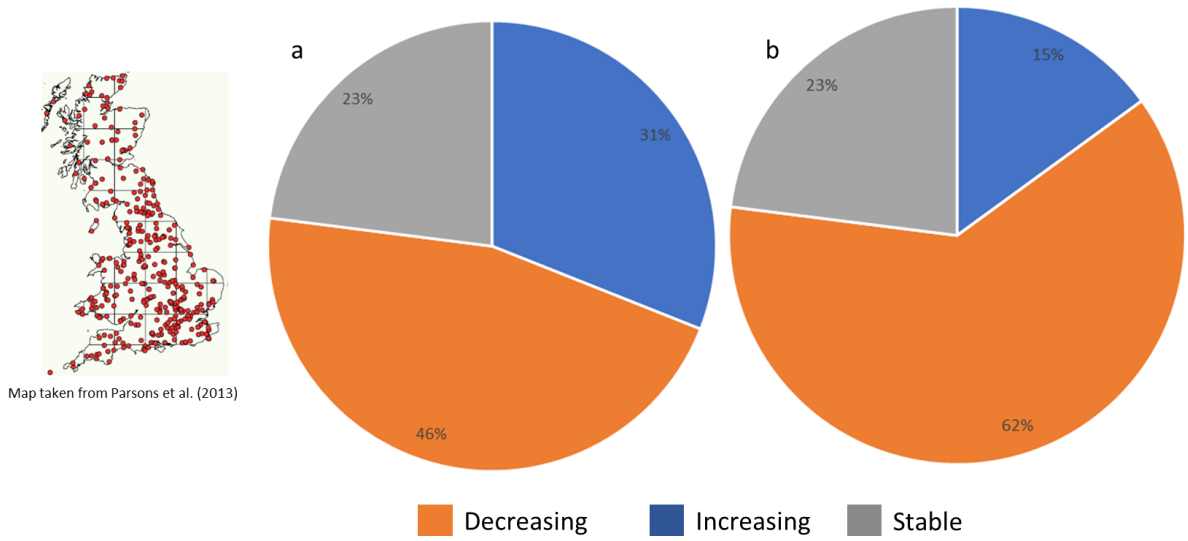

Figure 4.6 Map of Rothamsted trap locations (*n* = 80) used to collect moth trend data during a 40-year period between 1968 and 2007, and pie charts showing population trends for (a) consumed *B. barbastellus* macro-moth prey (*n* = 75) and (b) all monitored British macro-moths (*n* = 1086) (Fox et al., 2013).

4.4 Discussion

4.4.1 Ranging behaviour and foraging habitat selection

The tracked bats showed a large variability in individual MCP and foraging distances. This agrees with other studies on *B. barbastellus* (Greenaway, 2008; Hillen et al., 2009; Zeale et al., 2012; Kokurewicz et al., 2017) and highlights (i) the likely large required sustenance zone relative to other bats species and (ii) the capability of *B. barbastellus* to travel relatively long distances from roosting sites to foraging grounds (4.8 ± 2.7; range 1.2-8.3 km). MCP size is variable across published studies (Greenaway, 2008; Hillen et al., 2009; Zeale et al., 2012; Kokurewicz et al., 2017) and, in part, reflects the ability of the species to commute long distances on occasion (Russo et al., 2010). This is probably influenced by the characteristics of agriculturally intensified habitats at some of these study sites where bats may travel further than they would in non-fragmented landscapes.

I found that the MCP size was smaller than documented in other studies on *B. barbastellus* foraging behaviour (Greenaway, 2008; Hillen et al., 2009; Zeale et al., 2012; Kokurewicz et al., 2017), which included or exclusively tracked post-lactating females and male bats. My study mainly included pregnant and lactating bats which is a possible reason for the relatively small size of individual MCPs as the high wing loading of pregnant bats will restrict foraging range, and lactating females need to revisit the roost to suckle pups through the night (Henry et al., 2002; Womack et al., 2013), as was observed. This suggestion should be viewed with caution as the number of bats tracked was also small compared with other studies, and the combined colony MCP size will be related to the number of bats tracked if bats forage in different areas. Despite a variation in range sizes among studies, *B. barbastellus* can travel long distances even under times of reproductive stress, and appear to have limited barriers to movement when traversing a landscape, suggesting that the species is able to exploit fragmented landscapes (i.e. isolated foraging habitat within human-influenced landscapes). This contrasts with less mobile species such as *Myotis bechsteinii* that rarely cross barriers in the landscape such as roads (Kerth and Melber, 2008).

Core foraging areas were only 5.8 ± 3.7% of the total area used by tracked *B. barbastellus* and foraging areas had little or no overlap among individuals. This relatively small percentage of range use used has been documented previously for foraging *B. barbastellus* (Hillen et al., 2009; Zeale et al., 2012), and spatial segregation during foraging is evident across populations, with Zeale (2009) proposing that *B. barbastellus* may be territorial. Spatial segregation of individual foraging areas has implications for population ecology and the spatial scale needed for *B. barbastellus* management at the landscape scale, and is likely to increase distances travelled to foraging habitat.

The selection of foraging habitat was not random, with (in order) wetland, woodland and pasture being positively selected and arable, urban areas and moorland being least preferred. This trend was also observed by Zeale et al. (2012), who radio tracked post-lactating *B. barbastellus*, and indicates that despite variation in distance travelled and size of MCP, these habitats are selected for foraging

throughout the bats' active period, and that habitat selection is not influenced by reproductive state in females. The two most selected habitats are associated with high insect abundance, particularly riparian vegetation and broadleaved woodland, which support diverse populations of moths (Skinner, 2009; Waring and Townsend, 2009; Sterling and Parsons, 2012; Highland et al., 2013; Lintott et al., 2014c). The protection and restoration of bankside vegetation, wet meadows, wet woodland, and broadleaved woodland is important. The impact of surrounding landscape characteristics on foraging ground suitability should also be considered as urbanisation can reduce the quality of riparian zones up to 3 km away (Lintott et al., 2015b).

Pasture, which was dominated by improved grassland, may contain relatively few potential prey resources yet the habitat was positively selected for foraging in. This has been explained by the presence of features at boundaries such as hedgerows (Zeale et al., 2012). I observed the bats tracked at these habitats were indeed flying along hedgerows and minor tree lines, reinforcing the perceived value of these habitat features in the landscape. Although the telemetry procedure used lacks fine spatial resolution, it could be inferred that the consistent location of fixes deemed to be close to field boundaries confirms that the boundaries, rather than the grassland itself, is being used.

A core sustenance zone around the home wood should be created in which important habitat types can be conserved or enhanced for *B. barbastellus*. The most suitable way to establish a sustenance zone is to create a buffer around the home wood using the radius of the mean maximum range of the radio tracked bats (BCT, 2016). I found the core sustenance zone radius required for *B. barbastellus*, based on a subset of individuals from one maternity colony, is 4.8 km. This is smaller than advised using the results from multiple studies of *B. barbastellus* (6.5 km, n = 3 studies) (BCT, 2016). A more conservative approach could calculate the radii needed from measuring the furthest distance by any bat travelled, which results in an 8.6 km core sustenance zone. This would ensure more foraging habitat is conserved, but would require more than double the resources with potentially decreasing returns. Indeed, the use of furthest distance travelled by any bat is viewed as

resulting in too large an area for core sustenance zones as it will likely be affected by from outliers (i.e. if a single bat that travels a disproportionate distance compared to other bats) (BCT, 2016). When recalculating the core sustenance zone using the mean maximum range of all studies (*n* = 4 colonies; *n* = 78 bats) the advised core sustenance zone for *B. barbastellus* should cover a 5.8 km radius around the colony roosting site (i.e. home wood).

4.4.2 Diet composition

I found most prey items in the *B. barbastellus* faecal pellets were moths (97.5%). Although flies and lacewings were identified, their frequency (*n* = 3) would suggest that these species are not targeted by foraging *B. barbastellus*. Moth species were variable in size and consisted of large macro-moths (e.g. *Noctua pronuba*, wingspan 45-55mm) and small micro-moths (e.g. *Eudonia mercurella*, wingspan 16-19mm) with no obvious preference for any prey size. On average, a bat consumed six identifiable prey species, indicating plasticity for prey selection within the order Lepidoptera. The bats probably consume moth species which are abundant at the time. This is best evidenced by the larger amount of moths with increasing population trends in the diet of *B. barbastellus* when compared to all monitored moths (Conrad et al., 2004). Moths that are increasing may be more abundant, and hence more likely to be prey. *B. barbastellus* have evolved stealth echolocation through the reduction of echo intensity and further reduction in intensity level during their approach phase (Goerlitz et al., 2010; Lewanzik and Goerlitz, 2018), which probably allows them to prey more often on insects with simple tympanic ears that are sensitive to ultrasound and which can respond with evasive behaviour (Roeder, 1962). Whether they actively target moths with 'ears' or simply gain a fitness benefit from the ability to prey on these defence evolved species when other bats cannot is unclear. I found that 74% of the insects consumed by *B. barbastellus* were in families known to have simple tympanic ears (Roeder, 1974; Scoble, 1992; Fullard, 1998). This suggests that *B. barbastellus* benefits from an ability to capture moths with simple tympanic ears; although it may simply be that these species happen to be the most abundant at the time. I find that *B. barbastellus* is indeed a moth specialist (Goerlitz et al., 2010; Zeale et al., 2011; Lewanzik and Goerlitz, 2018) and is capable

of consuming both micro- (wingspan <20 mm) and macro- (wingspan >20 mm) moths. Any reduction in moth numbers will reduce their available food source.

The primers used to amplify the DNA extracted from faecal pellets (Zeale et al., 2011) are less suitable at targeting coleopteran species than other insect orders (Brandon-Mong et al., 2015) which may have resulted in the absence of beetles in my results, although previously undertaken traditional microscopic analysis of prey agrees with these molecular results i.e. a high proportion of moth parts (Zeale et al., 2011) and absence of beetles (Rydell et al., 1996).

4.4.3 Prey larval habitat

The importance of prey source habitat in bat conservation was studied at a breeding colony of *Rhinolophus euryale* (Mediterranean horseshoe bat) in the northern Iberian Peninsula (Arrizabalaga-Escudero et al., 2015). *R. euryale* is a moth specialist, and eats adult Lepidoptera which have larval host plants outside the bats' foraging grounds (Arrizabalaga-Escudero et al., 2015). This finding is of relevance to any species that target prey which undergo habitat shifts across ontogenetic life stages. When I investigated whether this phenomenon is relevant to *B. barbastellus* I found that 79% of consumed moths had larval host plants mainly within the bats' foraging habitats and a further 18% were generalists (i.e. had larval host plants that are abundant in habitats used by foraging *B. barbastellus* and in habitats that they avoid) leaving only 3% of consumed prey as mostly dependent on host plants within areas not used by foraging *B. barbastellus*. Unlike *R. euryale*, conservation effort could be focused only at *B. barbastellus* selected foraging habitat (i.e. woodland, wetland and grassland boundaries) without adverse impacts on most of their prey. There are limitations regarding spatial resolution with the data used in my research. More individual bats would need to be radio tracked to include finer-scale habitat categories for habitat compositional analysis. Although my conclusion is based on broad habitat types and may have different outcomes at a finer scale, 67% of the consumed caterpillars feed on host plants found in hedgerows (and because *B.*

barbastellus forage at hedgerows) I do not believe research at a finer scale would provide a different conclusion.

4.4.4 Prey conservation status and population trends

Long term monitoring (1968-2007) of British macro-moths has shown that overall abundance has decreased by 28% (Fox et al., 2013). This trend is heavily influenced by reductions in the south of Britain (40%), with total abundance reductions in the north being offset by northern range expansions of some species (Fox et al., 2013). This has relevance for moth specialists such as *B. barbastellus* that have a southern distribution within Britain. Our current understanding of *B. barbastellus* distributions and habitat suitability is based on presence records and MaxEnt modelling (Zeale, 2011), and the predicted distribution in Britain is related to mean summer temperature (15^{O}C or above) and total summer rainfall (250–300 mm or below) (summer refers to the warmest annual quarter) (Zeale, 2011), which limits their northern range. In Germany temperature had no contribution to model predictions however (Gottwald et al., 2017). The differences are likely due to latitudinal location. As *B. barbastellus* is at their northern limit of its range, limits to the northern range may be related to prey availability as well as climate, and *B. barbastellus* may have the potential to expand its range northwards.

The finding that a larger amount of moths with increasing population trends in the diet of *B. barbastellus* when compared to all monitored moths is encouraging. *B. barbastellus* appear to select prey that are abundant at the time and so increases in abundance of some moth species may reduce any potential negative effect of reductions in less abundant moth species.

4.5 Management recommendations

My findings provide evidence for the conservation management of *B. barbastellus* in an agriculturally dominated fragmented landscape at the northern edge of its global range. Landscape

features such as minor roads do not appear to reduce the nightly movements of *B. barbastellus*. *B. barbastellus* is a moth specialist, and the observed 40% decline in moth abundance over their range in southern England is cause for concern. *B. barbastellus* consumes moths that, as larvae and adults, require the same habitats as those selected by foraging bats. Creating, restoring and conserving *B. barbastellus* foraging habitat will also conserve their prey during all ontogenetic life stages.

Management should focus on the protection and enhancement of foraging habitats within a 5.8 km sustenance zone of maternity roosting sites including bankside vegetation, wet meadows, wet woodland, broadleaved woodland and secondary habitat such as hedgerows. Hedgerows are particularly important as they provide food for moth prey larvae, and are targeted by *B. barbastellus* while foraging, presumably due to their possession of structural characteristics that facilitate prey capture opportunities. The ranges of some moth species are expanding north as the climate warms. More research is needed to establish if the same northern movement is predicted, or occurring, for *B. barbastellus*.

4.6 Supplementary material

Table S4.6 List of identified prey species confirmed within the faecal pellets of *B. barbastellus* showing prey host plant habitat type as described in section 4.2.5, and Lepidoptera population trends since 1968.

Species	Host plant habitat	Reference used[ǂ]	Population trend[ǂǂ]	% of population change[ǂǂ]
Abrostola tripartita	Wetland, Woodland, Pasture	1	Increasing	108.2
Aethalura punctulata	Wetland, Woodland, Pasture	1	Stable	-20.8
Agonopterix heracliana	Wetland, Woodland, Pasture	1	no data	no data
Agrotis exclamationis	Wetland, Woodland, Pasture	3	Decreasing	-75.7
Agrotis ipsilon		3	Decreasing	-61.5
Agrotis segetum	Wetland, Woodland, Pasture	3	Decreasing	-66.5
Alcis repandata	Wetland, Woodland, Pasture	3	Stable	13.2
Amphipyra pyramidea	Wetland, Woodland, Pasture	1	no data	no data
Anaplectoides prasina	Wetland, Woodland, Pasture	1	no data	no data
Apamea monoglypha	Wetland, Woodland, Pasture	3	Decreasing	-21.7
Apamea sordens	Wetland, Woodland, Pasture	2	Decreasing	-40.5
Apocheima pilosaria	Wetland, Woodland, Pasture	3	Decreasing	-62
Archips podana	Wetland, Woodland, Pasture	2	no data	no data
Archips xylosteana		3	no data	no data
Asthena albulata	Wetland, Woodland, Pasture	1	Stable	73
Atethmia centrago	Wetland, Woodland, Pasture	1	Decreasing	-70.3
Autographa gamma	Generalist	3	Decreasing	-46.2
Biston betularia	Wetland, Woodland, Pasture	3	Decreasing	-66.4
Cabera pusaria	Wetland, Woodland, Pasture	1	Increasing	85.7
Cameraria ohridella		2	no data	no data
Caradrina clavipalpis	Generalist	3	Increasing	275.1
Caradrina kadenii			no data	no data
Caradrina morpheus	Wetland, Woodland, Pasture	1,2	Decreasing	-84
Carcina quercana		1	no data	no data
Catarhoe rubidata	Wetland, Woodland, Pasture	1,2	no data	no data
Cerastis leucographa	Wetland, Woodland, Pasture	3	no data	no data
Cerastis rubricosa	Wetland, Woodland, Pasture	3	Decreasing	-64.1
Charanyca trigrammica	Wetland, Woodland, Pasture	1	Stable	43.1
Chloroclysta miata	Wetland, Woodland, Pasture	1	Decreasing	-43.6
Chloroclystis v-ata	Wetland, Woodland, Pasture	1,2	Increasing	102.5
Coleophora kuehnella		2	no data	no data
Conistra vaccinii	Wetland, Woodland, Pasture	3	Increasing	51.9
Cosmia trapezina	Wetland, Woodland, Pasture	3	no data	no data
Cosmorhoe ocellata	Wetland, Woodland, Pasture	1	Decreasing	-22
Cryphia domestica		3	Increasing	297.5

Cryptoblabes bistriga	Wetland, Woodland, Pasture	1	no data	no data
Cucullia chamomillae	Wetland, Woodland, Pasture	1	no data	no data
Cyclophora annularia		2	no data	no data
Depressaria pastinacella	Wetland, Woodland, Pasture	2	no data	no data
Diarsia rubi	Generalist	3	Decreasing	-87.4
Drosophila melanogaster			no data	no data
Dysstroma truncata	Wetland, Woodland, Pasture	3	no data	no data
Ectropis crepuscularia	Wetland, Woodland, Pasture	1	Increasing	24.5
Electrophaes corylata	Wetland, Woodland, Pasture	3	Decreasing	-42.9
Endotricha flammealis		3	no data	no data
Epirrhoe alternata	Wetland, Woodland, Pasture	1	Stable	19.2
Eudonia lacustrata		1	no data	no data
Eudonia mercurella		1	no data	no data
Eulithis prunata	Wetland, Woodland, Pasture	1	Stable	2.4
Eupithecia abbreviata	Wetland, Woodland, Pasture	1	no data	no data
Eupithecia absinthiata	Generalist	1,2	no data	no data
Eupithecia exiguata	Wetland, Woodland, Pasture	1	no data	no data
Eupithecia plumbeolata	Wetland, Woodland, Pasture	1	no data	no data
Eupithecia subfuscata	Wetland, Woodland, Pasture	3	no data	no data
Eupithecia vulgata	Wetland, Woodland, Pasture	1	no data	no data
Euproctis similis	Wetland, Woodland, Pasture	3	Stable	-6.6
Eurrhypara hortulata	Wetland, Woodland, Pasture	1,2	no data	no data
Gymnoscelis rufifasciata	Generalist	2	no data	no data
Hemerobiidae spp.			no data	no data
Hemithea aestivaria	Wetland, Woodland, Pasture	2	Decreasing	-32.8
Herminia grisealis	Wetland, Woodland, Pasture	1	Decreasing	-28.9
Herminia tarsipennalis	Wetland, Woodland, Pasture	3	Decreasing	-24.5
Hoplodrina ambigua	Wetland, Woodland, Pasture	1,2	Increasing	432.6
Hoplodrina blanda	Wetland, Woodland, Pasture	1	Decreasing	-77.9
Hoplodrina octogenari	Wetland, Woodland, Pasture	2	Increasing	36.5
Hydriomena furcata	Wetland, Woodland, Pasture	1,2	Increasing	42
Hydriomena impluviata	Wetland, Woodland, Pasture	1	Stable	-7.7
Hypena proboscidalis	Generalist	1	Stable	3.7
Idaea aversata	Wetland, Woodland, Pasture	1,2	Increasing	22.6
Idaea biselata	Wetland, Woodland, Pasture	1	Stable	-8.1
Lampropteryx suffumata	Wetland, Woodland, Pasture	1	Stable	20.6
Lithophane socia	Generalist	2	no data	no data
Lomaspilis marginata	Wetland, Woodland, Pasture	1,2	Stable	-9.9
Lomographa bimaculata		3	Stable	73.1
Luperina testacea	Arable, Moorland, Urban	3	Decreasing	-44.2
Lymantria monacha	Wetland, Woodland, Pasture	1	Increasing	164.3
Mamestra brassicae	Generalist	1	Decreasing	-42.4
Maniola jurtina	Wetland, Woodland, Pasture	3	no data	no data
Mesapamea secalis/didyma	Generalist	3	Stable	18.7
Mythimna impura		1	Stable	-1.2

Nematopogon swammerdamellus		3	no data	no data
Noctua comes	Generalist	3	Increasing	86.5
Noctua fimbriata	Generalist	1	Increasing	984.3
Noctua pronuba	Arable, Moorland, Urban	3	Increasing	185.8
Noctua janthe	Generalist	3	Increasing	32.2
Nola confusalis	Wetland, Woodland, Pasture	3	Increasing	198.3
Notodonta ziczac	Wetland, Woodland, Pasture	3	no data	no data
Nycteola revayana	Wetland, Woodland, Pasture	3	no data	no data
Ochropleura plecta	Wetland, Woodland, Pasture	2	Stable	23.1
Odontopera bidentata	Wetland, Woodland, Pasture	3	Decreasing	-20.1
Oligia versicolor/strigilis	Wetland, Woodland, Pasture	1	no data	no data
Opisthograptis luteolata	Arable, Moorland, Urban	1,2	Decreasing	-37.5
Orthosia gothica	Wetland, Woodland, Pasture	3	Decreasing	-39.8
Orthosia gracilis	Wetland, Woodland, Pasture	1	Decreasing	-74.2
Orthosia incerta	Wetland, Woodland, Pasture	1	Decreasing	-37.3
Pammene fasciana	Wetland, Woodland, Pasture	1	no data	no data
Pandemis cerasana	Wetland, Woodland, Pasture	3	no data	no data
Peribatodes rhomboidaria	Wetland, Woodland, Pasture	2	Decreasing	-47.8
Perizoma affinitatum	Wetland, Woodland, Pasture	1	Decreasing	-47.1
Petrophora chlorosata	Wetland, Woodland, Pasture	1	Decreasing	-17.2
Pheosia gnoma	Wetland, Woodland, Pasture	1,2	Decreasing	-57
Phlogophora meticulosa	Wetland, Woodland, Pasture	3	Increasing	33.2
Polyploca ridens	Generalist	1	no data	no data
Pseudargyrotoza conwagana	Wetland, Woodland, Pasture	1	no data	no data
Rivula sericealis	Wetland, Woodland, Pasture	1	Increasing	9.2
Scathophaga stercoraria			no data	no data
Scoliopteryx libatrix	Wetland, Woodland, Pasture	3	no data	no data
Scoparia basistrigalis		2	no data	no data
Scopula floslactata	Generalist	1	Stable	-17.5
Selenia dentaria	Generalist	3	Decreasing	-64.1
Spaelotis ravida	Wetland, Woodland, Pasture	2	no data	no data
Spilosoma luteum	Wetland, Woodland, Pasture	3	Decreasing	-68
Thyatira batis	Wetland, Woodland, Pasture	1	Decreasing	-49.8
Trichopteryx carpinata	Wetland, Woodland, Pasture	1	Increasing	219.9
Udea lutealis		2	no data	no data
Xanthorhoe designata	Generalist	1,2	Increasing	86.5
Xanthorhoe fluctuata	Generalist	1,2	Decreasing	-75.2
Xanthorhoe montanata	Wetland, Woodland, Pasture	1	Decreasing	-48.39
Xestia c-nigrum	Wetland, Woodland, Pasture	2	Increasing	31.1
Xestia xanthographa	Generalist	3	Increasing	80

[ŧ]References include (1) HOSTS database (Natural HistoryMuseum, London (Robinson et al., 2010), (2) UK moths database (https://www.ukmoths.org.uk/), and (3) reference books (Skinner, 2009; Waring and Townsend, 2009; Sterling and Parsons, 2012).

[ǂ]Data collected by the Rothamsted Insect Survey (https://www.rothamsted.ac.uk/insect-survey). Population trends are considered 'decreasing' or 'increasing' only if significant (40 year period) (Fox et al., 2013).

CHAPTER 5

General Discussion

Sustainable certification through the UK Forestry Standard is driving forward a better way to manage woodland for biodiversity in the UK (FC, 2017). However, inevitably the guidance provided to forestry practitioners relies on an evidence base that has gaps, particularly for protected species such as bats (Russo et al., 2016). My research targeted the knowledge gaps that will best allow woodland managers to improve woodlands for bats. In agreement with Russo et al., (2010) I believe that we need to rethink the value of intensively managed woodland for bats, as focussing on optimal habitat such as old growth woodland, although important, ultimately results in isolated habitat of limited extent. Throughout most of Europe, old growth woodland represents less than 3% of approximately 45% woodland cover (FAO, 2012). Even woodland types that are poor for biodiversity and which are heavily exploited, such as fast growing and relatively short rotation conifer plantations, provide some ecological opportunities for bats (Kirkpatrick et al., 2017). It is mostly unclear how commercial woodland management affects bats and their insect prey. This limits our ability to provide 'bat friendly' production-managed woodland, or to confidently state that 'light touch' management or rewilding (Monbiot, 2013) is the only suitable approach.

Broadleaved woodland provides material with potential environmental benefits (i.e. wood-derived biomass material for heating and electricity) and is also identified as important wildlife habitat (Myers et al., 2000). Our ability to use multiple renewable technologies (including biomass derived from trees) is considered the only feasible way to remove the global reliance on fossil fuels (FAO, 2010). The extraction of wood-derived biomass by selective thinning has shown to directly influence the value of a woodland for wildlife (Taylor et al., 2013; Cistrone et al., 2015), and this must be balanced against the benefits of biomass, particularly in the UK where government is incentivising the reversion of abandoned and under-managed woodland into production (FC, 2015).

My research finds that (i) the conservation of woodland-dwelling bats primarily benefits from old aged woodland and these woodlands should be protected, (ii) unmanaged and minimal intervention managed woodland benefits bats by providing woodland characteristics that typically form in old age

woodland and are scarce in commercially managed woodland, and their value increases over time, (iii) commercially managed woodland does have value to bats and their insect prey but this can be greatly improved without minimising the impact on harvesting intensity, (v) conservation effort focused on foraging habitats selected by *B. barbastellus* will also conserve its prey species, and (vi) the moth species that *B. barbastellus* consume are declining in their UK range.

5.1 Providing opportunities for bats and their insect prey within broadleaved woodland

Intermediate and heavy woodland thinning reduces the amount of standing dead trees and the number of tree cavities. I found the presence of these woodland characteristics was important for all tree-dwelling bats and radio tracking showed that the abundance of tree cavities best explained roost site selection by the rare *B. barbastellus*. This has been shown in other parts of Europe (Russo et al., 2004; Hillen et al., 2010; Kortmann et al., 2017) and importantly it is likely that how these roosts form, and their characteristics, are less important than their frequency. I found that the probability of roost use increased as the number of cavities on a tree increased. Reproductive status influenced roost type section and roost switching. A colony of tree-dwelling bats requires roosts that provide different attributes such as temperature and the ability to move roosts when required. Indeed, *B. barbastellus* uses socio-thermoregulation to optimise roost temperature (Russo et al., 2017a) and this behaviour is facilitated by increased numbers of roosts.

Tree age is a unidirectional habitat filter (Pereira et al., 2004; Burgar et al., 2017) for tree-dwelling bats (i.e. roosting opportunity increases as a tree ages until it falls and decomposes), which was best evidenced by the finding that tree age is a driver of the number cavities on a tree and within a woodland. Sustainable woodland management guidelines recognise the value of standing dead trees to wildlife (FC, 2017) but the recommended minimum threshold value is unlikely to be sufficient to sustain viable colonies of tree-dwelling bats. More standing dead trees could be achieved in production woodland as they do not compete for resources, and should not affect the health or

growth of the economic stock through direct competition, although I acknowledge that standing dead trees can provide suitable habitat for tree pest species that could reduce the timber quality of neighbouring trees. Although ageing and standing dead trees are important to bats, I found that young trees with cavities were regularly used as roost trees. Any tree regardless of age or species that has at least one cavity will add value to a woodland for bats.

Woodland thinning can maintain heterogeneity of the canopy when compared with abandoned and minimal intervention managed woodland. This reflects well on the progress made toward wildlife sympathetic forestry providing structural variability (UKWAS, 2017), and highlights a move away from homogenously structured managed woodland (Lacki et al., 2007; Law et al., 2015; Russo et al., 2016). The response by bats to canopy architectural attributes such as openness and ruggedness was positive. The edge-adapted *P. pipistellus* selected woodland with increased canopy ruggedness, identifying the importance of foraging opportunity at the canopy for edge-foraging bats (Müller et al., 2013; Froidevaux et al., 2016). Light Detection and Ranging (LiDAR) imagery identified that *B. barbastellus* roosted in cavities on trees that were in woodland areas below relatively open canopies and although closed canopies may facilitate increased nightly foraging times (Russo et al., 2007), I believe the benefit of light penetrating the canopy and warming a potential roost is more important, particularly for juvenile bats.

Below canopy vegetation clutter was low in managed woodland, high in recently abandoned and minimal intervention woodland (*ca*. 30 years), and again low in woodland afforded no management for relatively long periods (65+ years). Common and adaptable edge species were more active in managed woodland presumably by taking advantage of less cluttered woodland interiors that facilitate manoeuvrability. The effect of dense below canopy clutter may also be larger in edge foraging species that are under reproductive stress as found in pregnant and lactating *P. pygmaeus* (Lintott et al., 2014a). The response by bats (richness and activity) to clutter followed hypothesised relationships (Lacki et al., 2007), with most bats showing reductions in activity in woodlands with

dense understory clutter regardless of whether all bats were grouped together, by echolocation guild or species. The only species not to show any negative trend with clutter density was *P. auritus* which highlights that this species is adapted for flight and prey capture success in dense woodland interiors (Patriquin and Barclay, 2003). *B. barbastellus* was less affected by clutter than other species despite being considered an edge foraging species, maybe reflecting its short-range echolocation characteristics (Zeale, 2011; Lewanzik and Goerlitz, 2018) or a stronger influence of tree cavity frequency. In contrast to bats, insect numbers peaked when woodlands were highly cluttered showing that moths (and flies (Fuentes-Montemayor et al., 2013)) benefit from below canopy vegetation clutter and woodlands with this characteristic may be important source habitats for two main bat prey groups. It would therefore be unsuitable to recommend a homogenously uncluttered below canopy structure despite the strong negative influence of dense clutter on bat richness. Providing pockets of cluttered understory vegetation within woodland that has relatively low understory vegetation clutter would be a suitable conservation management approach.

5.2 Providing opportunities for bats and their insect prey in the wider landscape

The suitability of the wider landscape should be considered both for its influence on woodland use by bats (Fuentes-Montemayor et al., 2013) and for facilitating commuting to suitable foraging habitat. Using molecular and telemetry techniques I was able to identify that *B. barbastellus* (i) appears to be unaffected by landscape barriers such as roads (although most of these were minor roads) (Kerth and Melber, 2008), (ii) that the bats do not select foraging grounds at random, and instead target areas of probable high prey abundance, including riparian zones, broadleaved woodland and linear features such as hedgerows, (iii) it is unlikely that *B. barbastellus* targets any particular species within the lepidopteran order, and instead is a generalist, taking moths that are abundant at the time which is facilitated by their evolved stealth echolocation trait (Lewanzik and Goerlitz, 2018), (iv) conservation management of the bats' foraging grounds will also conserve prey

larval habitat. This is an important consideration as not all bats select prey that depend on the same habitat throughout all their distinct ontogenetic stages (Arrizabalaga-Escudero et al., 2015), (v) *B. barbastellus* prey may be expanding their ranges north likely due to a warming climate encouraging greater numbers of prey more north (Fox et al., 2013).

The research methods used in my thesis were selected to control for variation of surrounding habitat types in the wider landscape by using a matched pair design to investigate the influence of woodland management. It is therefore important to highlight that bats and their prey respond differently to woodlands in different landscape matrices. For example, Lintott et al. (2015a) found that the relative abundance of sympatric species (*P. pipistrellus* and *P. pygmaeus*) in woodland changes with the level of urbanisation surrounding woodland, with *P. pygmaeus* showing a more negative response to urbanisation than *P. pipistrellus*. Female *P. pygmaeus* also select less fragmented woodlands when under reproductive pressure (Lintott et al., 2014a). I did not investigate intraspecific responses to woodland management type. Fuentes-Montemayor et al., (2012) found that woodland extent was the best predictor of moth abundance, and Lintott et al. (2014c) related this finding to a reduction of woodland edge exposed to the surrounding habitat. Isolation of woodland (Lintott et al., 2014a) and wider agri-environment schemes may also influence the use of woodland by some bat species, but not by others (Fuentes-Montemayor et al., 2011; J. Froidevaux, unpub. data). I recommend that forestry practitioners and conservation managers consider the influence of wider landscape alongside local scale recommendations.

5.3 The importance of time as a directional habitat filter

Bat species richness had a strong temporal relationship with time since last management. In the absence of over-grazing when a woodland is abandoned, inter and intra-specific competition between floral species as they compete for light and space results in below canopy clutter (Finegan, 1984). Woodlands that have been unmanaged for 30 years are densely cluttered (Adams et al.,

2009; Peterken and Mountford, 2017) and I found bat richness was at its lowest point at around 30 years since last management. After 30 years of no management, bat richness began to increase. A woodland in the early stages of succession will have a different value for bats than a woodland at a later stage of succession, and depends on a species' ecomorphological traits and reproductive state (Lintott et al., 2014a). As much as tree age is a unidirectional habitat filter for bats (section 5.1), time is a directional filter (i.e. the value of a woodland to bats increases from young established woodland scrub to old aged dynamic mature community woodland). The periods of time that unmanaged woodland were least suitable for most bats (i.e. highest level of understorey clutter) were however times when they were highly suitable for nocturnal insects.

It is feasible to consider that important habitat characteristics can be achieved in all broadleaved woodland by either encouraging woodland to succeed temporally by abandonment (although grazing control may be required), or by using minimal intervention management if invasive floral species are considered detrimental, or even managing production woodland to facilitate the development of important woodland characteristics. A more stand-off management approach that is often considered when discussing rewilding (Monbiot, 2013) would appear to be the best recommendation for the conservation of bats in European broadleaved woodland, although this limits any opportunity to use these woodlands for biofuel on an industrial scale which in itself is of environmental benefit.

5.4 Management recommendations

A number of management recommendations can be based on evidence presented in this thesis, and if implemented will contribute to the conservation of bats and their insect prey in woodlands.

1 Conserve semi-natural ancient and primary woodland

Old growth woodland is vitally important to woodland-dwelling bats and the preservation and restoration of these habitats should be a conservation priority. In the UK, ancient semi-natural broadleaved woodland should be retained and throughout Europe the removal or alteration of pristine (or primary) woodland is considered negative for bat populations.

2 Minimal intervention management

Promoting the natural succession of younger woodland will help to deliver additional sustained benefits in the future. A minimal intervention management approach will allow the natural maturation of the woodland and the gradual development of old growth characteristics, in particular standing dead trees and a more heterogeneous structure, features that are beneficial to bats. Woodland managed by minimal intervention will initially decrease the opportunity for bats due to dense below canopy clutter during early stage succession, but will be suitable for their insect prey during these periods.

3 Increase the amount of tree cavities

To promote biodiversity, the UK Woodland Assurance Standard (UKWAS) certification recommends $20m^3$/ha of standing and fallen deadwood to be present in sustainably managed woodland (UKWAS, 2017). This recommendation is insufficient and should (i) differentiate between fallen and standing deadwood, (ii) recommend $60m^3$/ha of standing deadwood volume as a minimum, and (iii) encourage managers to evenly distribute this volume of standing deadwood throughout a woodland.

To ensure more trees with cavities persist within a production woodland I suggest the promotion of positive selection (i.e. removing trees that directly compete with neighbour trees that are marked to remain) over negative selection (i.e. removing all undesirable trees including badly shaped trees such as those that are forked, bent, heavily branched or damaged).

4 Create a structurally diverse and open canopy architecture

A relatively open and heterogeneous canopy within mature woodland allows light to penetrate below the canopy and provides foraging opportunities in the canopy. Allowing light penetration though the canopy will warm roosts and encourage a species-rich understory that will benefit some bat species and insects (particularly moths) by providing a food source for their larvae.

5 Create a structurally diverse and uncluttered below canopy structure

Reducing below canopy clutter will increase bat species richness and activity by providing opportunities for open and edge foraging species to exploit the woodland interior, as well as for species adapted to foraging in the woodland interior. Insect abundance increases in woodland with high densities of below canopy clutter either by providing more foliage for their larvae or by reducing predation by aerial insectivores. To ensure suitability for both bats and their prey, pockets or strata of highly cluttered understory vegetation within woodland that has relatively low understory vegetation clutter is the best approach to adopt.

6 Landscape-scale conservation

The location of woodland within the landscape and surrounding landscape habitat type is important and should be considered in addition to these recommendations. Stakeholders should (i) establish core sustenance zones (BCT, 2016) which incorporate the range of bat species of interest, (ii) identify and protect core foraging habitats within these sustenance zones, (iii) identify the diet of each bat and ensure suitable habitat for insect prey (as adults and larvae) is protected. For the rare woodland bat *B. barbastellus*, conservation management policies should target the protection and

enhancement of riparian habitat, broadleaved woodland and linear landscape features such as hedgerows within a 5.8 km radius of roost sites. These habitats and features within the landscape should be managed to improve their value to foraging bats and all developmental stages of their moth prey. The population trends of these prey need to be monitored at this bat's northern range margin, particularly in southern England.

Unmanaged old growth woodland is important and young woodland should be encouraged to succeed naturally. The importance of old aged unmanaged woodland should not detract attention from the value of production woodland, particularly in countries with overall low woodland cover. It is possible to extract wood from woodland while still providing opportunity for wildlife. If this extracted wood reduces the burning of fossil fuels the changes observed in insect distributions and population shifts may be reduced and alleviate pressure on their predators. UK forestry is achieving biodiversity sympathetic production woodland, although the value of these woodlands can be greatly improved by encouraging practitioners to increase the frequency of woodland characteristics that are important to woodland dependent wildlife such as bats and moths.

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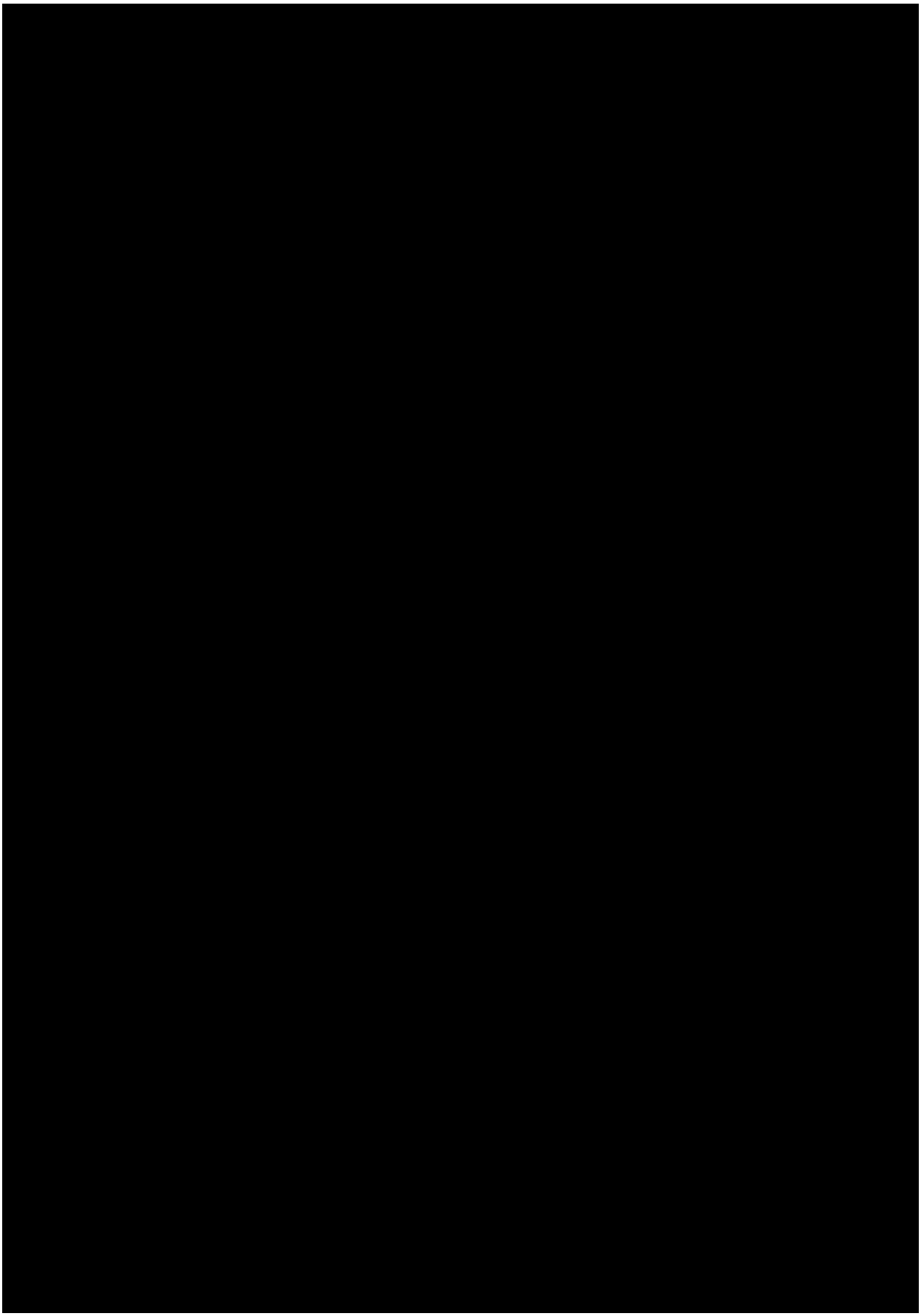
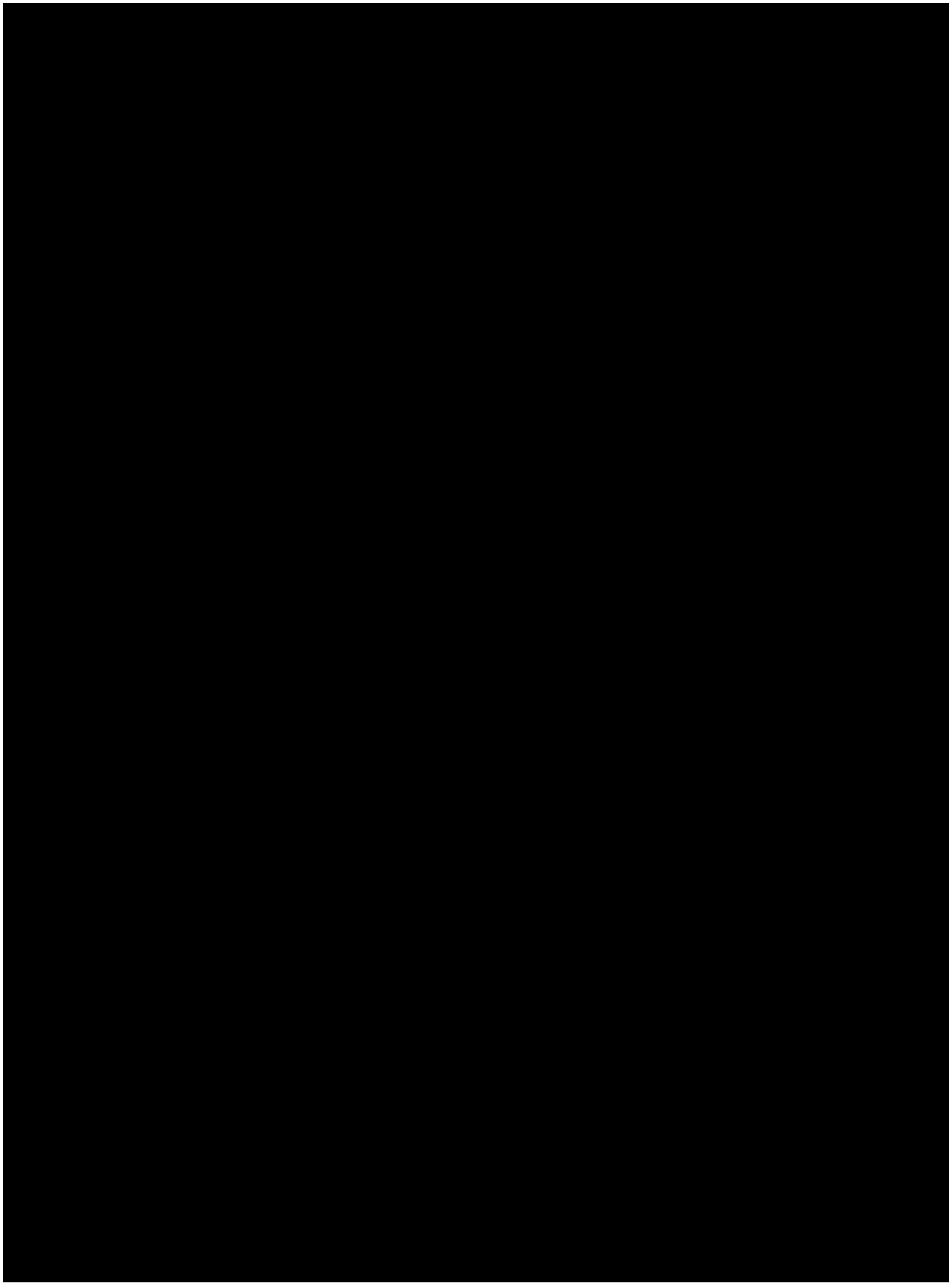
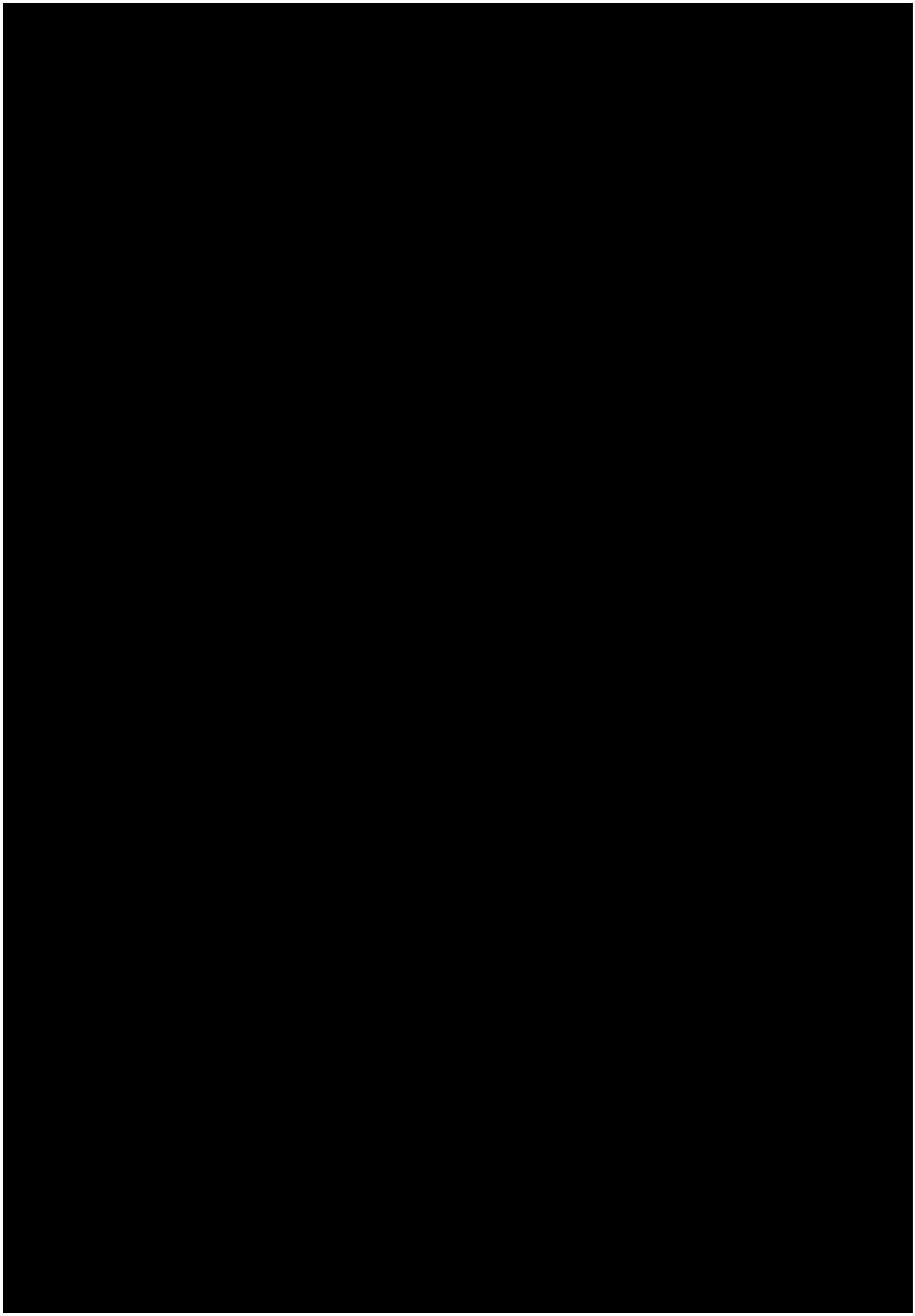
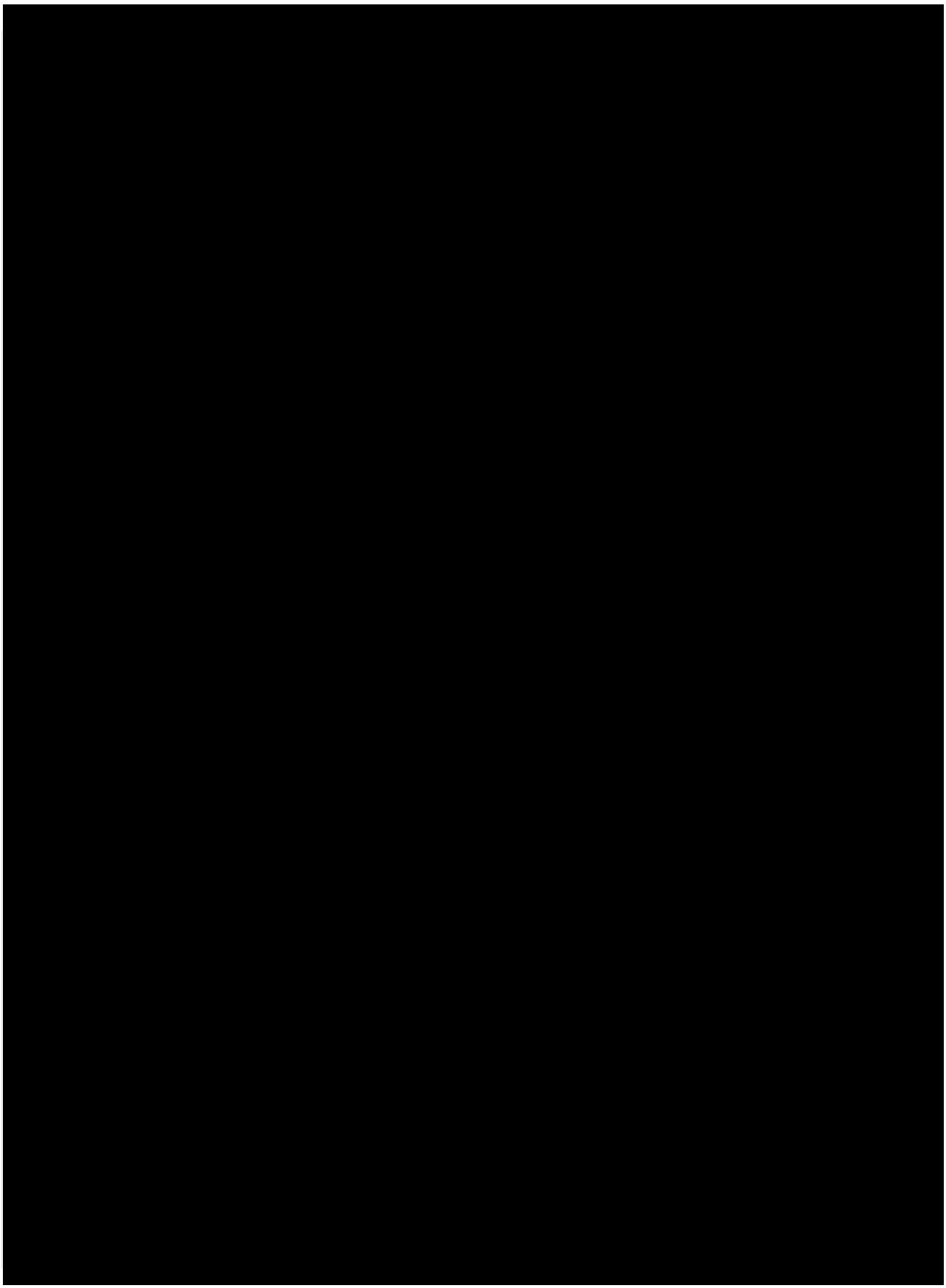
APPENDIX A

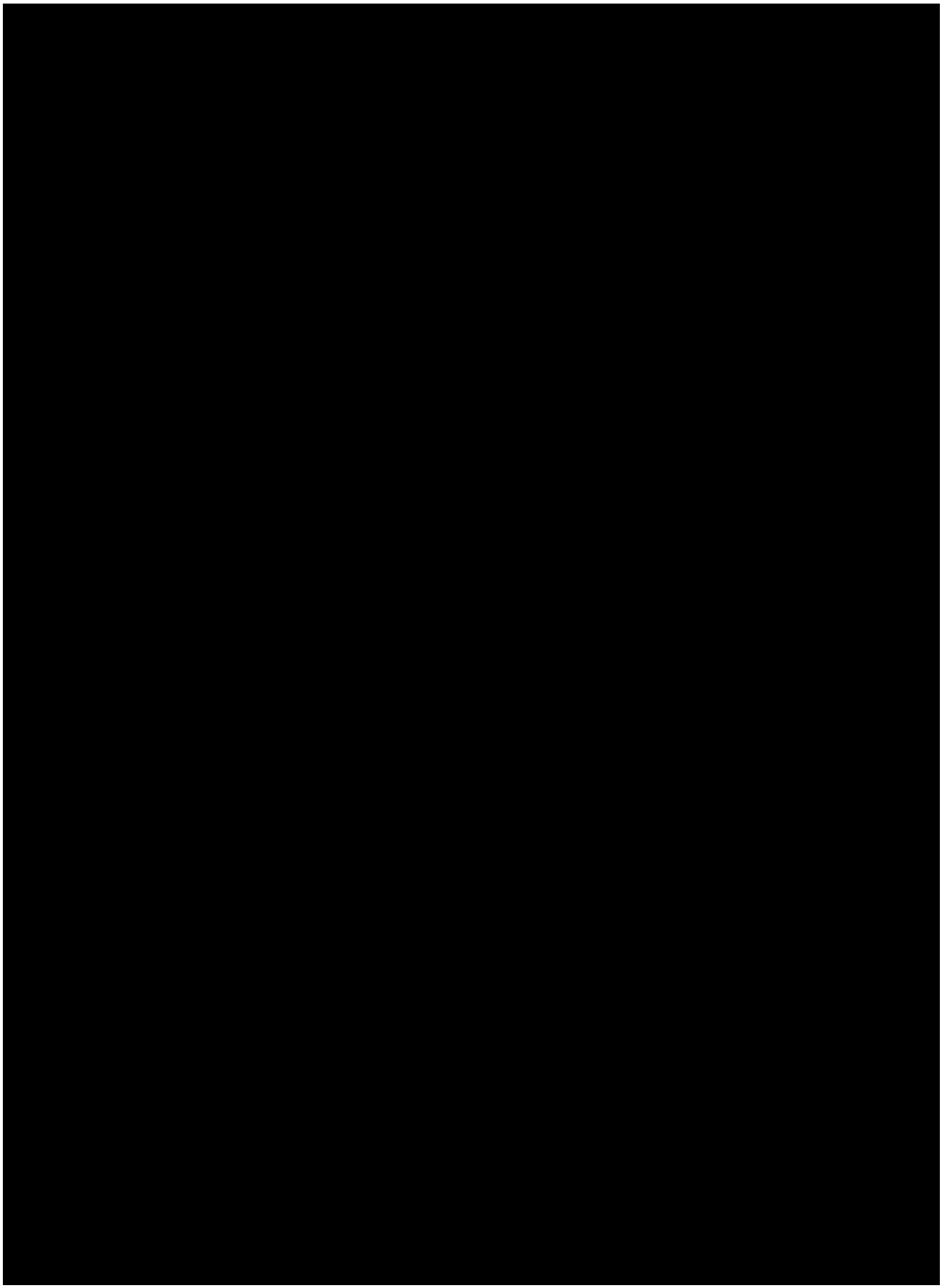
Published manuscript - Ground-based and LiDAR-derived measurements reveal scale-dependent selection of roost characteristics by the rare tree-dwelling bat *Barbastella barbastellus*. For. Ecol. Manage. 417, 237–246

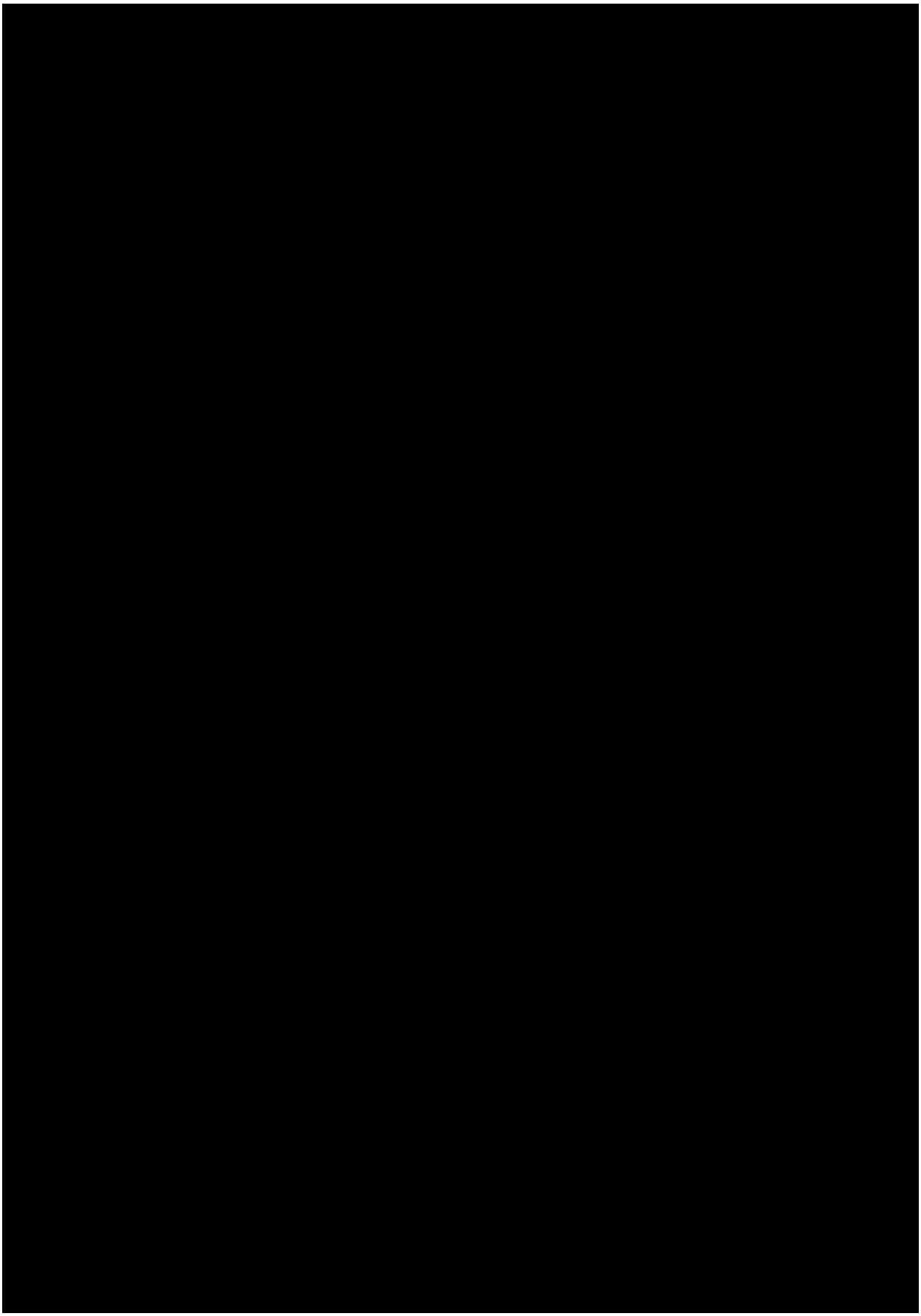


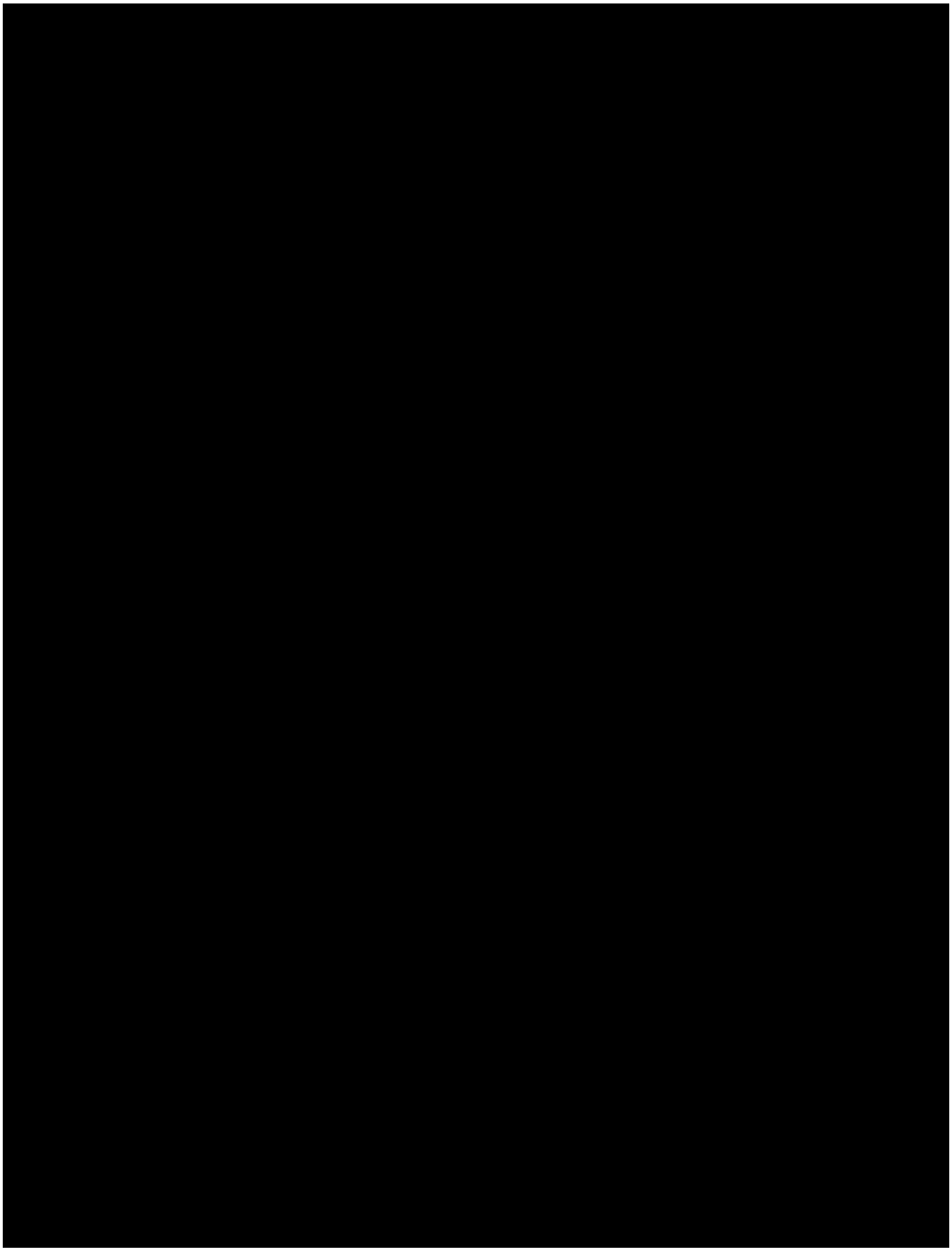


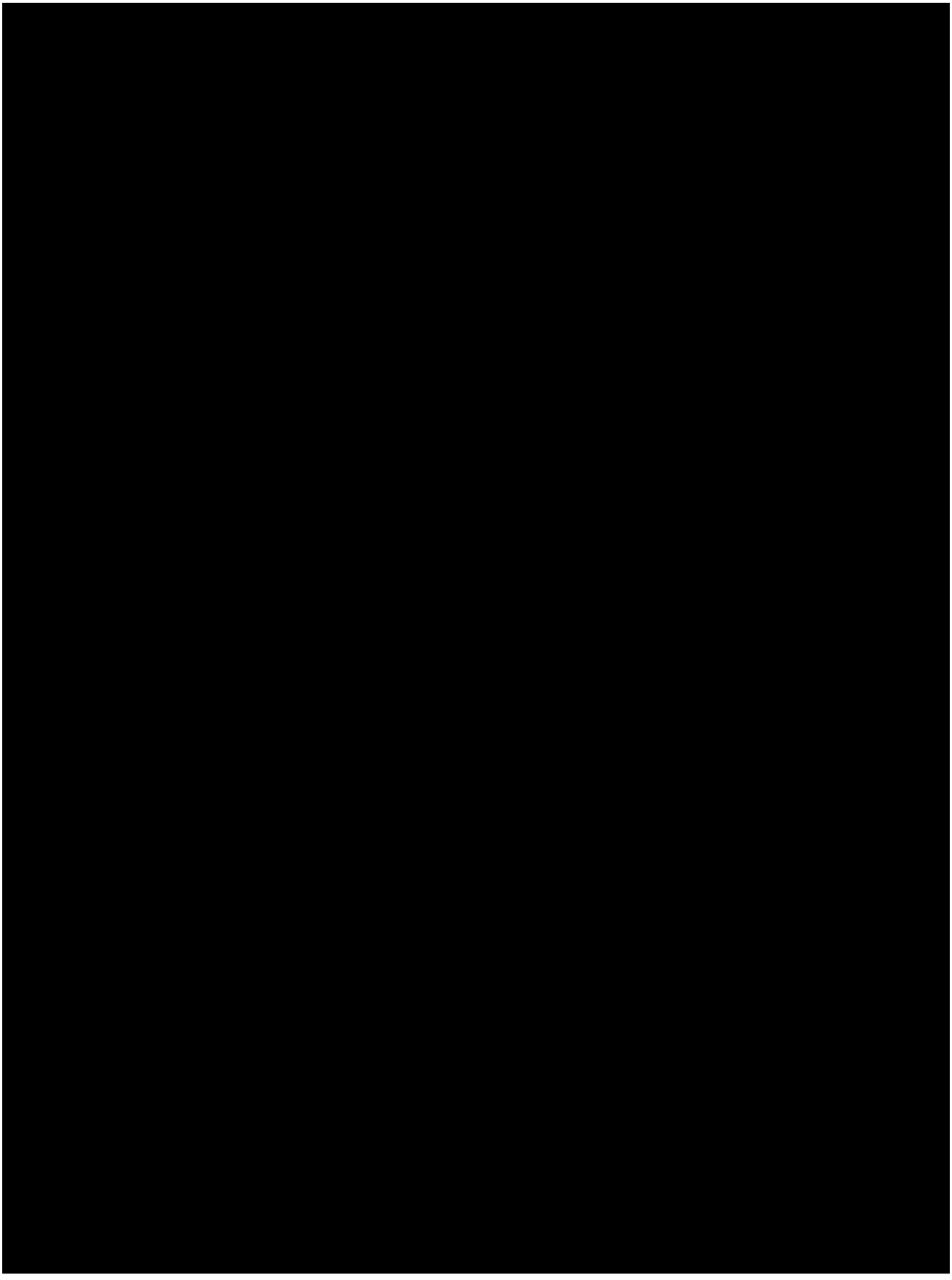


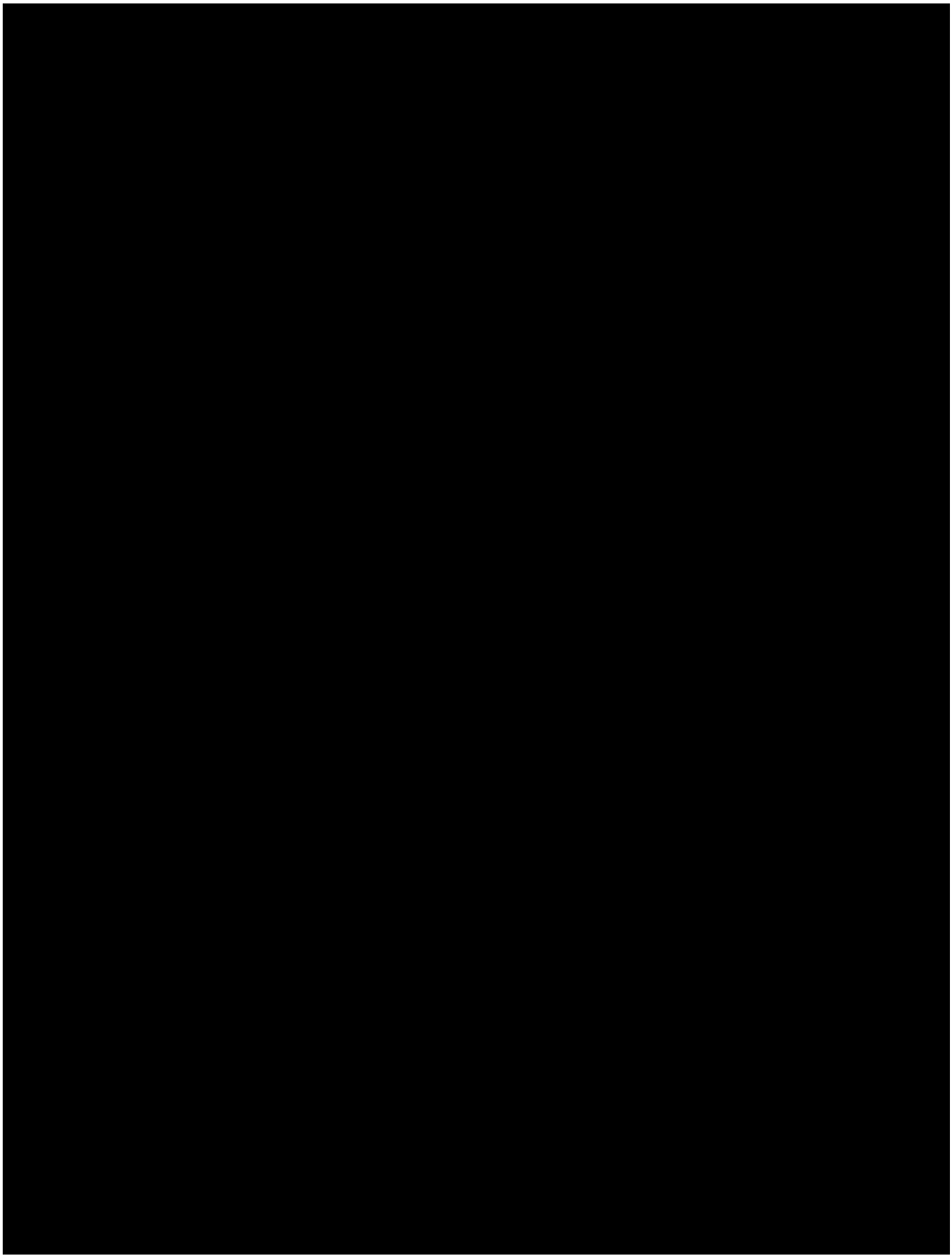












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APPENDIX B

Published manuscript - CCTV enables the discovery of new barbastelle (*Barbastella barbastellus*) vocalisations and activity patterns near a roost. Acta Chiropt. 20, 263-272.